

THE DIPLOPORITA OF THE OSLO REGION, NORWAY

by J. FREDRIK BOCKELIE

ABSTRACT. The Ordovician diploporite fauna from the Oslo Region is examined morphologically and taxonomically. The brachioles of *Protocrinites* are shown to be biserial. Pore-structures are described, including peripore connections and the structure of the skeletal mesh work. Internal morphological structures indicate a possible basal nerve ring and oral ring structures. Aspects of ontogeny and phylogeny dealt with include changes in plate number, an increased complexity of pore structures, and possibly an increased complexity of brachioles. A new family Parasphaeronitidae is described, comprising two new genera intermediate between Sphaeronitidae and Holocystitidae on the one hand and Aristocystitidae on the other. Fifteen taxa from three families are described, including three new genera (*Tetreucystis*, *Parasphaeronites*, and *Pachycystis*) and nine new species (*Protocrinites rugatus*, *Haplosphaeronis bratterrudensis*, *Eucystis langoeiensis*, *Tetreucystis kalvoeyensis*, *T. elongata*, *T. tetrabrachiolata*, Sphaeronitidae sp. A, *Parasphaeronites socialis*, and *Pachycystis norvegica*). The stratigraphical and geographical distribution of genera and species within the Oslo Region is compared with the type of sediment in which they occur. Many genera have a relatively wide stratigraphical and geographical distribution but individual species are restricted. Morphological variation is relatively great and phylogenetic changes within the Norwegian diploporites are probably very complex.

THE term cystoid is a collective name for certain echinoderms found in marine strata of Ordovician, Silurian, and Devonian age. Cystoids possess a bladder-like body (theca) of plates with respiratory pores. In the oral area they generally bear a number of food-gathering appendages (brachioles). A stem may be present but many forms, particularly among the class Diploporita, were directly attached to any available substrate by the basal plates of the theca. The echinoderm nature of cystoids was pointed out as early as 1772 by the Swedish miner J. A. Gyllenhaal in his studies of *Sphaeronites pomum* and *Echinospaerites aurantium* (Regnéll 1945, p. 1). Later von Buch distinguished them as a separate group of echinoderms. Paul (1972) dropped the name Cystoidea and elevated the two previous orders Rhombifera and Diploporita to class rank. Several questions regarding the morphology and taxonomy of diploporites remain unanswered. The question whether or not they are referable to the subphylum Blastozoa (Sprinkle 1973, pp. 57, 186) is answered in the present study by the discovery of biserial brachioles in *Protocrinites*.

Norwegian cystoids are often so well preserved that fine details of morphology can be studied; ontogenies, phylogenetic trends, and relationships to lithologies can be demonstrated. Detailed geological mapping, combined with a compilation of stratigraphical and geographical distributions within the Oslo Region (text-fig. 1), enables the relationship between echinoderms and lithofacies to be studied. The only previous comparable studies in Europe were restricted to Estonian rhombiferans *Hemicosmites* (in relation to reefs, Männil 1966) and *Echinospaerites* (distribution, Orviku 1927). The large numbers of *Haplosphaeronis* from the Gagnum Shale and the Gagnum Limestone (lower Ashgill) of Hadeland have enabled both ontogeny and variation within the genus to be studied. This is important in understanding aspects of phylogeny (see Bockelie 1978a).

STRATIGRAPHICAL OUTLINE

Norwegian diploporite cystoids are restricted to the middle and upper Ordovician (text-figs. 2-4); their appearance is sometimes more or less synchronous with those elsewhere, such as in Britain, Sweden, and Estonia. A comprehensive stratigraphical outline for the Oslo Region has been given by Henningsmoen (1960). The Cambro-Silurian sequence has been divided into ten units termed Stages; the Cambrian comprising Stages 1-2d,



TEXT-FIG. 1. Ordovician outcrops in the Oslo Region of Norway, central Sweden, and the Baltic states (black).

the Ordovician 2e-5b, and the Silurian 6-10. It has long been suggested that Stage boundaries are diachronous in the Oslo Region. This diachronism applies in particular to the Silurian, but it has also been proved for the Ordovician (Brenchley and Newall 1975; Owen 1978, 1979; Bruton and Owen 1979). The stratigraphical nomenclature whereby lithological units are named after their contained dominant fossil is now under revision by the author and others, and will be replaced by a lithostratigraphic terminology based on geographic names. In most areas the new formations will coincide with the previous stage names. The former use of a combination of numbers and letters for the stages is not continued here but is occasionally referred to in parentheses to allow comparison with previous work; published formation names are used. For the northern part of the Oslo Region references are made to Skjeseth (1963). Where no published names are available, the fossil names originally applied to the lithostratigraphic units are retained (Brøgger 1887).

The Oslo Region is generally considered to be an intracratonic depression in a Precambrian basement (Størmer 1967) with carbonate and terrigenous sediments on the Balto-Scandian foreland; a Precambrian land mass is considered to have been the source of the terrigenous sediments. Recent dating of the Ordovician sediments of Oslo-Asker confirms a Precambrian age for the source rock (S. Jacobsen, pers. comm.). Carbonate sedimentation prevailed in the more stable parts of the Balto-Scandian basin, including the middle Ordovician of central Sweden. Sedimentation rates in the Oslo Region appear to have been variable and sporadic influxes of mud flows to its more central portions have preserved some faunas more or less in life position.

MATERIAL, METHODS, AND PRESERVATION

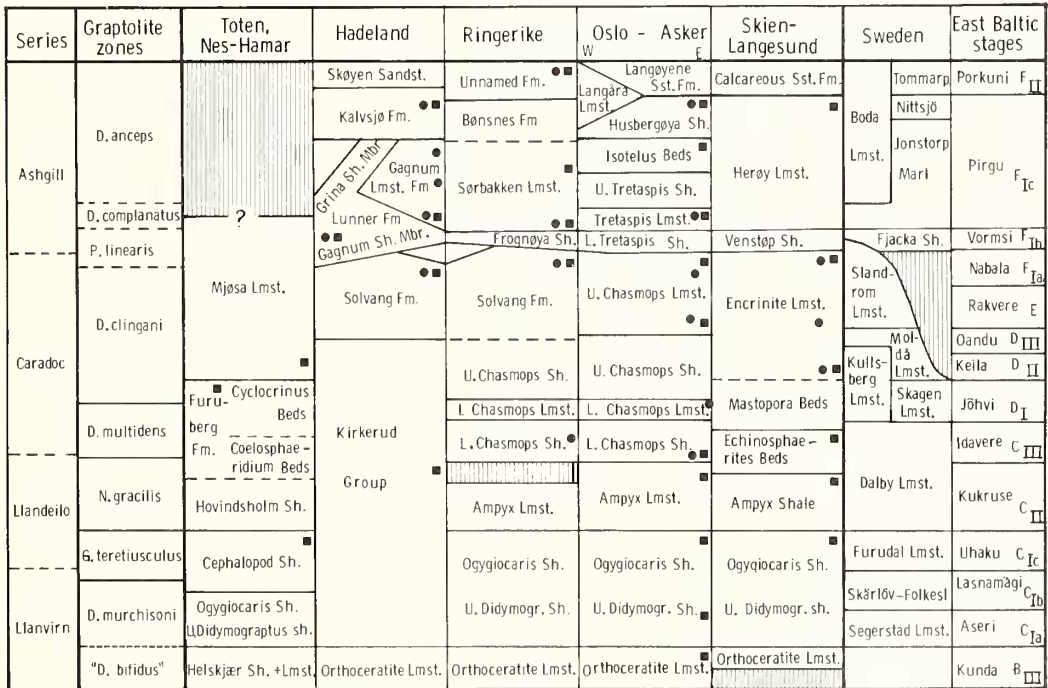
Previously, museum collections of Diploporita were very limited and consisted mainly of *Haplospiraonia kiaeri* from the lower Ashgill. Since 1966 more than one thousand cystoids have been collected from the Oslo Region, together with large numbers of other echinoderms. Some of these have been described by Bockelie (1973, 1979a, 1981) and Bockelie and Briskeby (1980). Large slabs were collected and usually decalcified using hydrochloric acid. The decalcified material was impregnated under one-third of atmospheric pressure. Casts were made from

silicone rubber. This method made it possible to study structures which could not have been detected by mechanical preparation, e.g. the brachioles of *Protocrinites* (text-fig. 13; Pl. 1). The casts were studied using stereophotographs and camera lucida drawings. Some drawings were made directly on to photographs and the photographic emulsion removed. Thin sections and serial sections were made to reveal peripore connections and plate meshwork. Some acetate peels were made, particularly from *Parasphaerontes socialis* n. gen., n. sp. Standard staining methods were used to increase contrast between the primary and secondary calcite.

When preserved in shales, the cystoids are either flattened or preserved as impressions; in limestones they are often well preserved and undistorted. In the upper Ordovician Husbergoya Shale (= Stage 5a), the cystoids weather more rapidly than their silty matrix (about 80-85% quartz) and are suitable for casting. Thecae are generally incomplete but the diploporites are usually more complete than the commonly disarticulated rhombiferans. Replacement and infilling of the cystoid test is common. Many specimens of different taxa show various degrees of pyritization. Often the pore canals and the skeletal meshwork is filled with microcrystalline pyrite. In such cases, connections of diploporite canals and other internal features may be preserved (text-fig. 20i). Pyritic membranes found within the thecae may be traces of mesenteries. I suggest that this type of preservation results from rapid burial in sediments of low permeability. Pyrite may have formed during subsequent decay in a slightly reducing environment. Further pyritization occurred during later diagenesis.

Several cystoid plates, particularly from the reef environments, are filled with asphalt and thus impregnated. This must have occurred after the decay of organic material, but before the formation of secondary calcite. Asphalt has also been found in fossils from the non-reef environments of the middle Ordovician of Gåsoya in Bærum, Landøya in Asker, and Langesund in the southern part of the Oslo Region; the bitumen may be derived from a local source.

Silicification of cystoids is not common, but does occur in a few localities (Tønnerud, Hadeland) in the lower Ashgill, often in coarse-grained sediments where bryozoans, brachiopods, and corals are also silicified (Bockelie and Bockelie 1971). Silicification of the echinoderms is of two types: (1) coarse-grained and mostly partial; (2) fine-grained showing good surface details. Oral and basal portions were silicified before the rest of the theca,



TEXT-FIG. 2. Stratigraphical chart of the Oslo Region and correlations with Sweden and the Baltic. Compiled data from Skjeseth (1963), Owen (1978), Bruton and Owen (1979), Brenchley and Newall (1975), Henningsmoen (1960), Männil (1966), and Williams *et al.* (1972). Black squares—distribution of rhombiferans; black dots—distribution of diploporites.

Series	Graptolite zones	Estonian stages	S. Norway Fm.	DISTRIBUTION OF ECHINODERM CLASSES IN S. NORWAY									
Ashgill	D. anceps	Porkuni F _{II}	Langøyene sst. Fm.										
		Pirgu F _{Ic}	Husbergøya sh.										
			Isotelus beds										
	D. complanatus		U. Tretaspis sh.										
	P. linearis	Vormsi F _{Ib}	L. Tretaspis sh.										
Caradoc	D. clingani	Nabala F _{Ia}	U. Chasmops lmst.										
		Rakvere E											
		Oandu D _{III}	U. Chasmops sh.										
	D. multidentis	Keila D _{II}											
		Johvi DI	L. Chasmops lmst.										
		Idavere C _{III}	L. Chasmops sh.										
Llandeilo	N. gracilis	Kukruse C _{II}	Ampyx lmst.										
	G. teretiusculus	Uhaku C _{Ic}	T. bronni beds Ogygiocaris sh.										
Llanvirn	D. murchisoni	Lasnamägi C _{Ib}	U. Didymogr. sh.										
		Aseri C _{Ia}											
	D. bifidus	Kunda B _{III}	Endoceratid lmst. Asaphus sh.										
Arenig													

TEXT-FIG. 3. Stratigraphical distribution of Ordovician echinoderm classes in the Oslo Region. Stratigraphical data as for text-fig. 2.

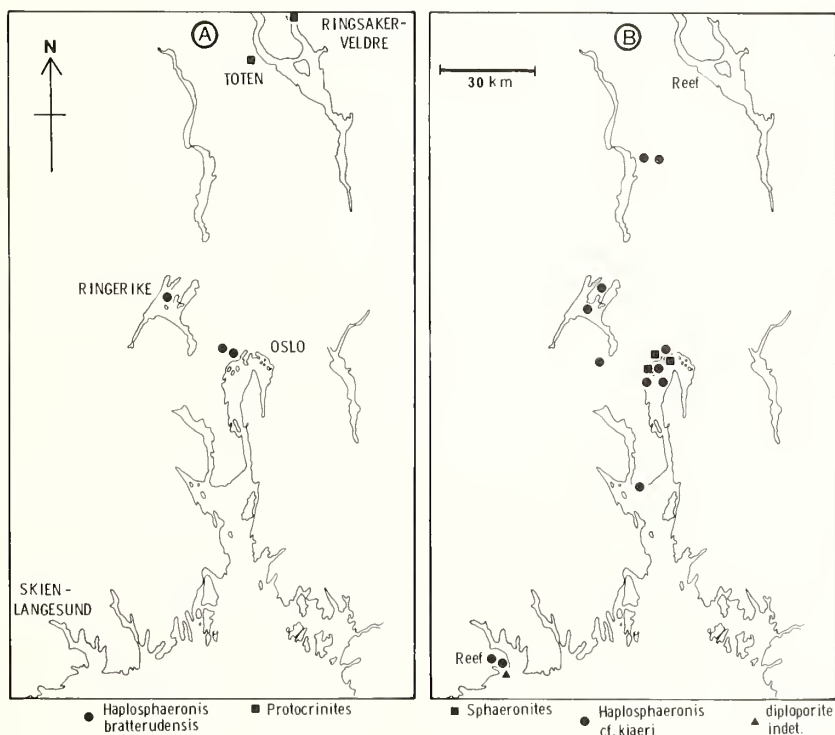
Series	Graptolite zones	Estonian stages	S. Norway Fm.	Distribution of Diploporita					no. of taxa
Ashgill	D. anceps	Porkuni F _{II}	Langøyene sst. Fm.						9
		Pirgu F _{Ic}	Husbergøya sh.						
			Isotelus beds						
	D. complanatus		U. Tretaspis sh.						
	P. linearis	Vormsi F _{Ib}	L. Tretaspis sh.						
Caradoc	D. clingani	Nabala F _{Ia}	U. Chasmops lmst.						
		Rakvere E							
		Oandu D _{III}	U. Chasmops sh.						
	D. multidentis	Keila D _{II}							
		Johvi DI	L. Chasmops lmst.						
		Idavere C _{III}	L. Chasmops sh.						
Llandeilo	N. gracilis	Kukruse C _{II}	Ampyx lmst.						
	G. teretiusculus	Uhaku C _{Ic}	T. bronni beds Ogygiocaris sh.						
Llanvirn	D. murchisoni	Lasnamägi C _{Ib}	U. Didymogr. sh.						
		Aseri C _{Ia}							
	D. bifidus	Kunda B _{III}	Endoceratid lmst. Asaphus sh.						
Arenig									

TEXT-FIG. 4. Stratigraphical distribution of diploporite genera in the Oslo Region and number of taxa in the lower, middle, and upper Ordovician.

as observed by Chauvel (1941). Silicification started from both the inside and the outside of the theca. Most of the silicified Norwegian specimens have a rather ghost-like appearance due to incomplete silicification. There may have been two periods of silicification, the first close to the time of burial, and a later one usually of the coarse-grained type.

DISTRIBUTION AND COMPARISON WITH FAUNAS ELSEWHERE

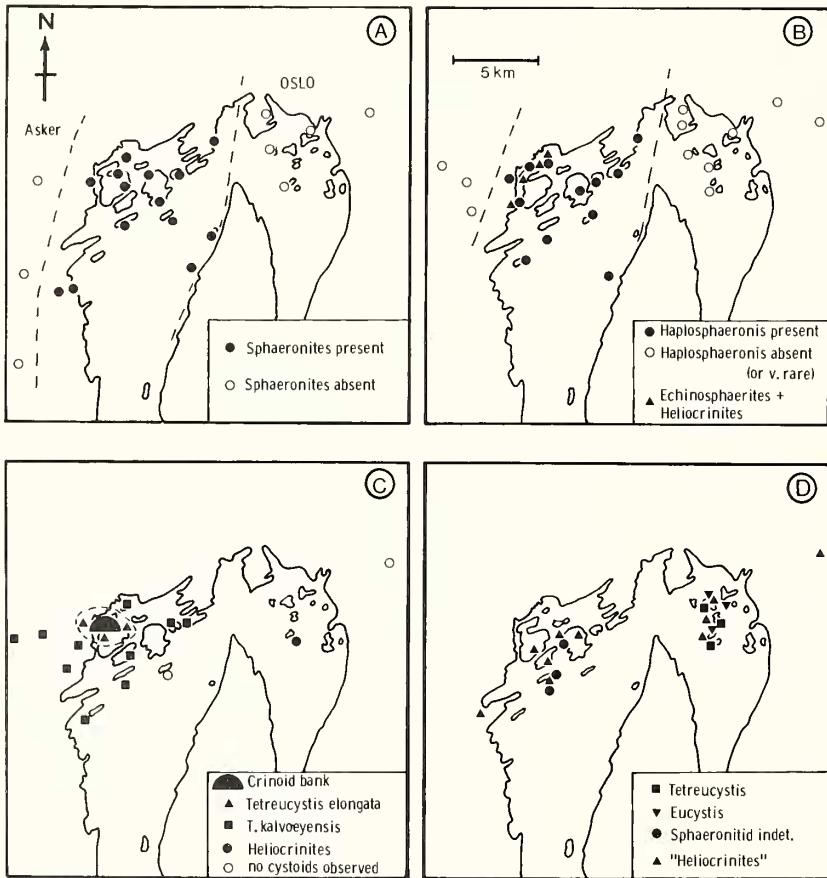
The echinoderm fauna of Norway is both extensive and diverse. Ten classes are known from the Ordovician of the Oslo Region (text-fig. 3), most of upper Ordovician age; echinoderms range from the Arenig to the Wenlock, but Diploporita are restricted to the Caradoc and Ashgill. Genera and species are restricted both stratigraphically (text-fig. 4) and geographically (text-figs. 5–7); most of the fifteen taxa present are found within a formation, and some in one locality only. The earliest known diploporite in the Oslo Region is *Haplosphaeronis bratterudensis* n. sp. (text-fig. 4), synchronous with *H. 'oblonga'* in the Dalby Limestone of Jämtland and Dalarna, Sweden. *Haplosphaeronis* is one of the most common diploporite genera in Sweden and Norway and ranges from the Caradoc to the middle-upper Ashgill. Its geographic and stratigraphic distributions depend on which of the original facies types are preserved. In the north Estonian confacies (Jaanusson 1976) *Haplosphaeronis* has never been found. However, in the Dalby Limestone of the central Baltoscandian confacies it has been recorded from several south Estonian borings (Männil 1966, figs. 13, 14), appearing at about the same stratigraphical level as in central Sweden (Dalarna). *Haplosphaeronis* occurs in the lower Ashgill of Britain (Paul 1973, p. 3) and Belgium (Regnéll 1951).



TEXT-FIG. 5. Geographical distribution of diploporites in the Oslo Region. A, in the *gracilis* Zone–*multidens* Zone. B, in the Lower Chasmops Limestone and equivalents (*Sphaeromites*) and in the *clingani* Zone.

In Estonia and Ingermanland three species of *Protocrinites* are known from the Arenig to the Caradoc. The genus is also found in the northern part of the Oslo Region at Brummundal (*Coelosphaeridium* beds of the Furuberg Formation; *peltifer* Zone). *Sphaeronites* is also restricted in Norway. *S. (Periaphros) pauciscleritatus* is present in the Lower Chasmops Limestone of Asker and Bærum (text-figs. 5B, 6A). I suggest that this species was restricted to a narrow ecological niche. In Sweden, *Sphaeronites* ranges from the late Arenig or Llanvirn to middle or upper Ashgill, and several species are known. In Estonia one or possibly two species occur in the Uhaku and Keila (Rõõmusoks 1970; Hecker 1964). Outside the Baltoscandian area, *Sphaeronites* is only known with certainty from the lower or middle Ashgill of Britain (Paul 1973; Paul and Bockelie 1983).

Beyond the Oslo Region, *Tetreucystis* is known only from the Ashgill of Sweden and Britain. *Archaeogocystis* (text-figs. 2, 4) is restricted to the Ashgill of Norway and Britain, and to the Llanvirn of Bohemia. *Eucystis* is locally present in the upper Ashgill of Oslo (text-fig. 6D), is relatively common in the Ashgill of Sweden and Britain, and occurs in the Ashgill of Bohemia and Spain (Chauvel and Le Menn 1979). It also occurs in the Devonian of Bohemia and North Africa, but has not been located in the Silurian.



TEXT-FIG. 6. Geographical distribution of cystoid genera in the Oslo-Asker District, showing the limits of certain genera. A, *Sphaeronites* in the Lower Chasmops Limestone. B, *Haplosphaeronites*, *Echinospaerites*, and *Heliocrinites* in the Upper Chasmops Limestone. C, cystoids in the Lower Tretaspis Limestone. D, cystoids in the Husbergøya Shale Member.

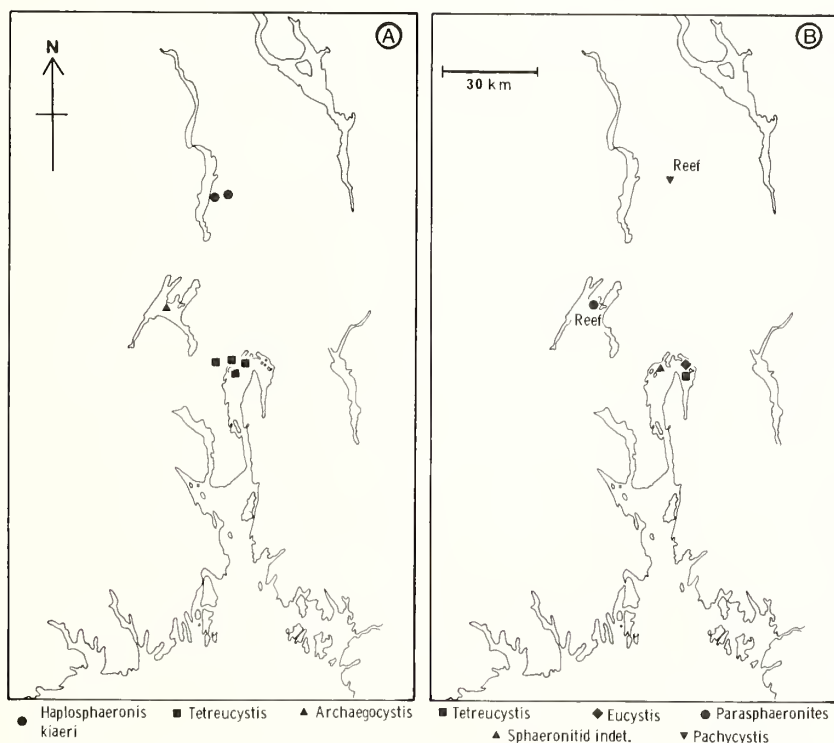
The diversity of the Diploporita increased from the lower to the upper Caradoc and from the lower to the upper Ashgill, coinciding with two major regressions in the Oslo Region. Consequently, I suggest that these cystoids were present in relatively shallow water, where several ecological niches were present (see later).

Diploporite cystoids first found their way into the Oslo Region in the late Kukruse Stage (text-fig. 2) and reached a first maximum diversity and expansion in the late Oandu-early Rakvere Stage. Another immigration took place in the Nabala Stage, reaching maximum expansion and diversity by the Porkuni Stage (text-fig. 2). Similar patterns can be demonstrated with other faunal elements (Bruton and Owen 1979). Diploporita were absent from the Oslo Region in the Arenig-lower Caradoc, whereas six taxa were present in the middle-upper Caradoc and nine taxa in the Ashgill. Patterns of geographical distribution of genera (text-figs. 5-7) are comparable with those of other fossil groups, both in the early Ordovician (Skjeseth 1952) and the middle Ordovician (Stormer 1953).

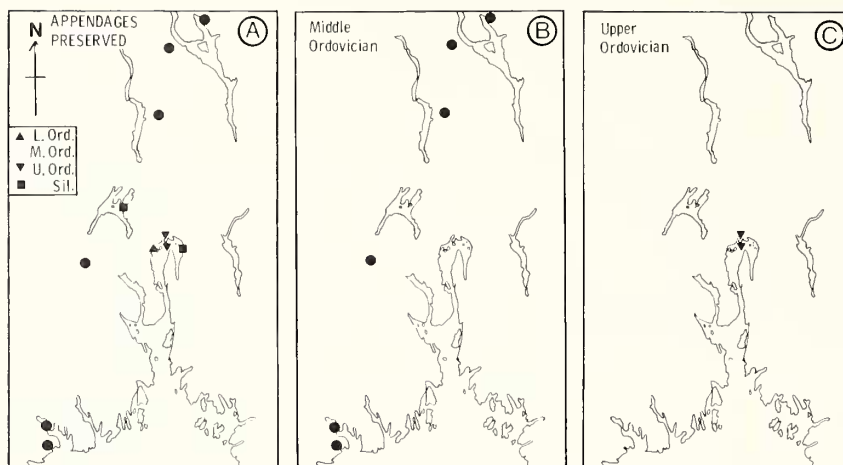
FAUNAL ASSOCIATIONS AND THEIR RELATIONSHIP TO SEDIMENT TYPE

The sediments within large areas of the Oslo Region are well exposed. Formations can be traced continuously for 15-20 km along strike; the distribution of species has been mapped (text-figs. 5-7). Detailed studies were made in Oslo-Asker, but only limited information exists for the rest of the Oslo Region because only parts of the area have been mapped in detail.

The preservation of echinoderms with brachioles and arms indicates that the animals were not transported far after death and before burial. The fauna was most probably periodically covered by rapid influxes of sediment. Echinoderms with appendages preserved are found in the westernmost areas in middle Ordovician sediments.



TEXT-FIG. 7. Geographical distribution of diploporites. A, in the *linearis* Zone. B, in the *anceps* Zone.



TEXT-FIG. 8. Areas where echinoderms have been found with appendages preserved (typically in areas of irregular sedimentation, and usually high sedimentation rate). A, Ordovician and Silurian. B, middle Ordovician only. C, upper Ordovician only.

and in the central Oslo-Asker part of the basin in upper Ordovician sediments (text-fig. 8). Diploporite genera and species, together with their faunal associations, are listed below; lithologies are also described and an interpretation of the environment is given.

Haplosphaeronis bratterudensis association. This is found in the Lower Chasmops Shale. The shale is interbedded with limestone beds, often planar and 5–10 cm thick. In Ringerike, where *Haplosphaeronis* is common, the shale is calcareous. The bioclastic content of the shale is slightly less than 20% in this area, decreasing to below 10% eastwards towards Oslo. Both the frequency of limestone beds and the carbonate content of the shale decrease in the same direction. The eastern limit of the faunal association is in Asker, about 20 km west of Oslo. Moving south-west from Ringerike the clay content of the sediment decreases and the rock becomes more bioclastic; these sediments are the result of a mixture between low and high sedimentation rates, and lack the *Haplosphaeronis* association. North-east of Ringerike the Lower Chasmops Shale grades into a shale with incursions of 20–50 cm thick sandstone beds which, from Hadeland northwards, also lacks *Haplosphaeronis*.

The fauna associated with *H. bratterudensis* is characterized by trepostome bryozoans (*Diplotrypa* sp.), trilobites (*Chasmops conicophthalma*, *Neoasaphus ludibundus*, *Iliaenus* sp., *Atractopyge dentata*), various brachiopods (including *Christiania hohtedahli*, *Eoplectodonta*(?) *percedens*, *Strophomena norvegica*), cephalopods (*Triptoceras*? *problematicum*), bivalves (*Cyrtodontula dubia*, *Ambonychia* aff. *amygdalina*, *Cunamyia multistriolata*, *Grammysia* sp.), gastropods (*Kokenispira estona*, *Helicotoma* sp.), ostracodes (*Ullerella hohtedahli*), eocrinoids (*Bockia heintzi*), and crinoids (*Ristnacrinus* sp. and others). The fauna probably lived on a soft bottom, with moderate to low current velocities, below wave base in an offshore environment, and in the proximal part of the basin.

Protocrinites rugatus association. This is approximately contemporaneous with the *H. bratterudensis* association and occurs *in situ* at only one locality, in the Coelosphaeridium Beds, Furuberg Formation, in the Veldre-Ringsaker area (text-figs. 2, 4). The association has also been found in a loose block at Toten (text-fig. 5A). The cystoids occur in a silty shale interbedded with cyclic deposits of fine-grained quartz sandstones, 20–50 cm thick. The sandstones only occasionally contain fossils but the shales are usually very fossiliferous with a bioclastic content of 2–25%.

Other echinoderms associated with *Protocrinites* include several undescribed crinoids, eocrinoids (*Rhipidocystis norvegica*), rhombiferan cystoids (*Cystoblastus*? sp.), and more than two genera of Asterozoa. The remaining fauna comprises brachiopods (*Sowerbyella ringsakerensis*, *Mjoesina* cf. *mjoesensis*, *Kiaeromiena* cf. *juvenilis*, *Hedstroemia* aff. *robusta*, *Leptaena*(?) *indigena*, *Kjerulfina* sp., *Strophomena hirsuta*, *S. steinari*, *Eostrophaeodonta williamsi*), trilobites (including *Chasmops conicophthalma*, *Iliaenus* cf. *glaber*, *Neoasaphus ludibundus*?, *Calyptaulax* sp., and calymenids), algae (*Mastopora concava*, *Coelosphaeridium cyclocrinophilum*), and bryozoa (*Diplotrypa* sp.). The fauna lived on a soft bottom with terrigenous clay in an offshore environment.

A periodic influx of fine-grained sand killed the fauna from time to time. Such periodicity and high sedimentation rates prevailed in the northernmost part of the Oslo Region during the early Caradoc and may represent storm action and/or microtectonic activity (Bockelie 1978b).

Sphaeronites (Peritaphros) pauciscleritatus association. This is present in the Lower Chasmops Limestone (text-figs. 2, 4) and is restricted geographically and stratigraphically (text-figs. 5B, 6A). It is found approximately 6 m above the base of the formation in 75 cm of nodular limestones. Macroscopically there is little difference between that part of the formation with *Sphaeronites* and that without, but microscopically there is a difference in bioclastic content (about 8–10% bioclastics in rocks containing *Sphaeronites*). Beyond the eastern limit of *Sphaeronites*, there is a decrease in both the carbonate and bioclastic content of the rock. Beyond its western limit the carbonate content increases slightly, and bioclastic content exceeds 15% before decreasing again further west.

The small numbers of *Sphaeronites* at each locality (3–10 per m²) suggest *in situ* populations. Most of the associated fauna has not been described, but it includes bryozoans (mostly stick bryozoans and small spherical colonies), brachiopods (including *Platystrophia* sp., *Kiaeromena* sp., *Sowerbyella?* sp., and various orthids), trilobites (*Chasmops conicophthalma*, *Dionide* sp., and calymenids), and crinoid ossicles (*Encrinites snarocensis?* type). There is a clear dominance of filter-feeders.

The area where *Sphaeronites* is found was a submarine topographic high during most of the middle and upper Ordovician (Bockelie 1978b). The sediments may have been locally consolidated in small patches and acted as a relatively firm substrate for stem-bearing organisms, including the cystoids and crinoids. The environment was possibly one of low sedimentation rates, or even local erosion, because small phosphate nodules and remanié deposits occur locally.

Haplosphaeronis cf. *kiaeri* associations. These have a wide distribution in the Oslo Region. Future research may prove that more than one species is present. At present the associations are known from the Encrinites Limestone and its equivalents in the Skien-Langesund area (text-figs. 2, 5B), Ringerike, Hadeland, Oslo-Asker (text-fig. 6B), and elsewhere; these may all be contemporaneous (text-figs. 2, 4). *Haplosphaeronis* always occurs in sediments containing a mixture of calcareous shales and nodular limestones but its relationship to sediment type has only been fully studied in Oslo-Asker (text-fig. 6B). The pattern of distribution between Asker and Oslo is similar to that observed for *Sphaeronites* (text-fig. 6A). *Haplosphaeronis* is found both in bioclastic pockets in the limestones and in the interbedded shales. Specimens in the limestones are often sediment-filled and show signs of short transport. In the shales, however, they are filled with calcite and show no signs of transport. The distributional pattern of *Haplosphaeronis* coincides with a presumed slight elevation on the sea bottom which, during deposition of the top of the Upper Chasmops Limestone, was within a zone of reworking by currents. Breccias and stromatolite-like structures have been found.

Associated with *Haplosphaeronis* cf. *kiaeri* in Asker are trilobites (*Chasmops extensa*, *Platyfichas laxatus*, *Stenopareia glaber*, *Lonchodomus* aff. *pennatus*, *Pseudosphacrexochus bulbosus*, *Calyptaulax* aff. *norvegicus*), several undescribed bryozoans (including *Diplotrypa* sp., stick-bryozoans, and thin almost dendritic types), brachiopods (including *Ptychoglyptus* aff. *munstcri*, *Hedstroemia* sp., a sowerbyellid and orthids), and ostracodes (*Platybolbina* sp.); a rugose coral *Coelostylis toernquisti* may occasionally be found (B. Neuman, pers. comm. Jan. 1980). Other echinoderms, including loose plates of *Cheirocrinus* s.l. and crinoid ossicles have been found in some localities.

The somewhat variable environments in which *H.* cf. *kiaeri* occurs represent a regressive stage of the sedimentary basin. It seems that most of the faunas were living below the zone of regular wave action in most areas. The environment was one of low sedimentation rates, occasionally non-deposition or even erosion. Some of the limestones were exposed at times, allowing the attachment of bryozoa and crinoids. Periodically the environment received influxes of carbonate-rich mud and bioclastic sand, probably after storm deposits or as mass flows. Such deposits are commonly found in Asker.

Haplosphaeronis kiaeri association. *H. kiaeri* has only been found in the calcareous Gagnum Shale and the overlying Gagnum Limestone (text-figs. 2, 7A) in the Ashgill of Hadeland. The best exposures are found at Tonnerud by Lake Randsfjord where detailed investigations (text-fig. 9B) indicate that *H. kiaeri* lived in both environments represented. The animals were rapidly covered by sediment after death which helped to preserve the details. The sedimentation rate was irregular, and periodically coarser elastics were brought into the otherwise quiet bottom conditions.

In the Gagnum Shale the associated fauna consists of bryozoans (mostly *Diplotrypa* sp.), numerous brachiopods (including *Mjoesina mjoesensis*, *Leptaena minuta*, *Platystrophia* sp., *Porambonites* sp.), other echinoderms (including a dendrocystid, cheirocrinids, edrioasteroids such as *Cyathotheca*, and crinoids such as

Ristnacrinus sp.), several trilobites (including *Tretaspis* of the *hadelandica* type and *Stygina minor*), and ostracodes (*Euprimites kahalensis*, *Bullaeferum* n. sp., *Balticella?* sp.). In the nodular Gagnum Limestone the associated fauna is more varied, with more than thirty recorded taxa of brachiopods (M. Bassett, pers. comm. Oct. 1979). It usually contains 2–5% bioclastic material, with bryozoans and rugose corals (*Coelostylis* n. sp.: B. Neuman, pers. comm. Jan. 1980) also making up an important part of the fauna. The limestone represents a more shallow water environment than the Gagnum Shale.

Archaegocystis occurs in the lower Ashgill, Sørbakken Limestone of Ringerike (text-figs. 2, 4, 7A); it derives from Frognoya and occurs in a nodular limestone somewhat similar to the Lower *Tretaspis* Limestone of Oslo-Asker. The interbedded shales in the Sørbakken Limestone are calcareous and often contain pyritized fossils. The limestone itself is a fine calcisiltite-calcimicrite which contains frequent *Chondrites* burrows and bears numerous *Planolites* traces. The associated fauna consists of trilobites (including *Tretaspis hadelandica*), a few orthid brachiopods, stick bryozoa (rare), and crinoid ossicles (not common). The sediments were deposited below wave base and are occasionally interbedded with coarse clastics which form thin bands at irregular intervals.

Tetreucystis elongata association. This is restricted to the nodular *Tretaspis* Limestone (text-figs. 6C, 7A) of Ashgill age on and around the island of Nesøya, west of Oslo. It surrounds a presumed topographic high on the sea floor, containing a crinoid bank (Bockelie 1978b), and may have lived in an unstable environment where bottom currents were relatively strong. It is unknown whether or not drifting of the populations occurred, but individuals are often found together in patches. Some specimens have been found growing on top of dead individuals, and it may be assumed that they lived close together. The only other fossil remains occurring commonly with *T. elongata* are trace fossils (*Chondrites*), and occasional trilobites (calymenids).

Tetreucystis kalvoeyensis association. This is contemporary with the *T. elongata* association and had a much wider geographical distribution (text-fig. 6C). Several populations of *T. kalvoeyensis* show little, if any, post-mortem transport. At Kalvøya in Bærum, west of Oslo, more than one hundred specimens were found together, associated with molt stages of trilobites (*Brachyaspis*), trace fossils (*Planolites* and *Chondrites*), and occasional cephalopods. The limestone has a low faunal diversity and seems to have formed in a shallow water environment. Quartz content is high (10–15%) and the average grain diameter is about 100 μm (three times larger than the average Ordovician grains from that same area). When traced further eastwards towards Oslo, cystoids become very rare. On the island of South Skjørholmen, in the Oslo fjord, a specimen of *Heliocrinites* was found (text-fig. 6C).

Tetreucystis tetrabrachiolata association. This is found in the uppermost part of the Husbergøya Shale (text-figs. 4, 6D). The Husbergøya Shale is silty with a quartz content of 20–35% (100 μm average grain size) and carbonate content of 25–50%. It can be traced for more than 15 km along strike, and there is a gradual change from Oslo towards Asker, both in coarseness of the sediments and the fossil content. *T. tetrabrachiolata* is found exclusively on the islands in Oslo (text-fig. 6D). Associated fauna consists of trilobites (*Dalmanitina mucronata*, *Tretaspis sortita*, *Stygina latifrons*), conularids, *Cornulites* worms, occasional brachiopods, and echinoderms (including *Eucystis langøeyensis*, '*Heliocrinites balticus*', and various crinoid ossicles). The sediments are heavily bioturbated, but show a relatively low faunal diversity; they seem to have formed well below wave base.

When traced westwards, the Husbergøya Shale on the islands in Asker contains an unidentified sphaeronitid cystoid. Sphaeronitidae sp. A. is found in sediments of relatively high bioclastic content and its associates suggest more shallow water than that in which *Tetreucystis tetrabrachiolata* and *Eucystis langøeyensis* occurred. The associated fauna in Asker consists of a trilobite (*Dalmanitina mucronata*), numerous brachiopods (more than ten taxa are being described by L. R. M. Cocks), bryozoans (stick and mat forms), and occasional rugose corals; associated echinoderms are '*Heliocrinites balticus*' (usually overgrown by bryozoa) and frequent crinoid ossicles of at least two types. *Cornulites* and worms have also been located. The sediments are heavily bioturbated.

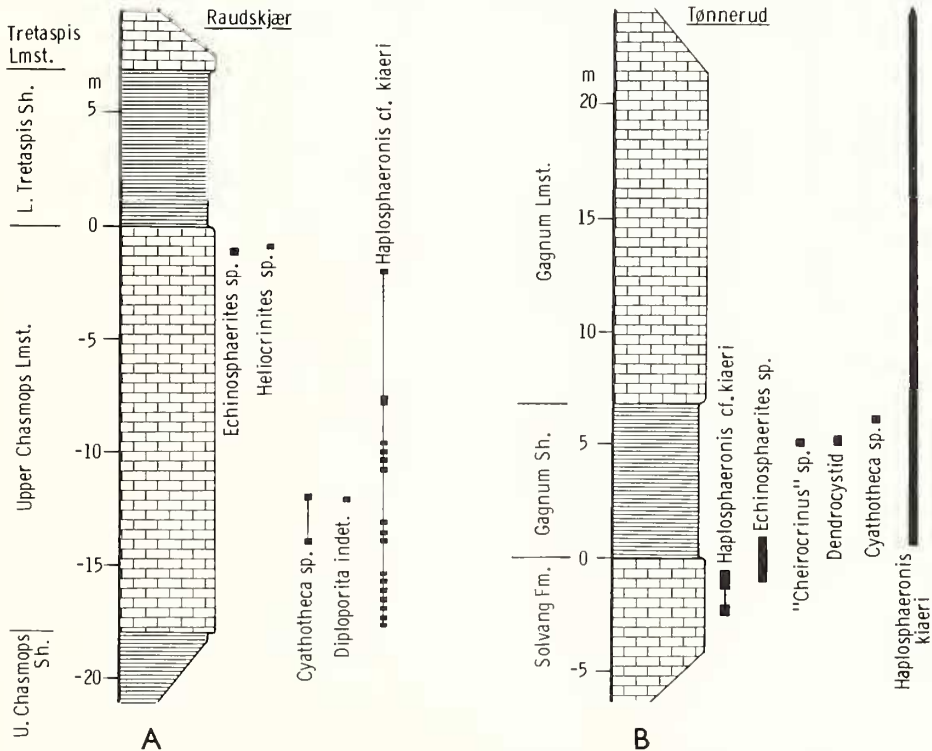
Two other diploporite genera from the Ashgill have a restricted distribution, *Pachycystis* n. gen. and *Parasphaeronites* n. gen. In the Kalvsjø Formation at Kalvsjø, Hadeland (text-figs. 2, 4, 7B), *Pachycystis* n. gen. occurs on the flanks of a carbonate mud mound. The terrigenous mud of the flanks is fine grained and has a calcium carbonate content of approximately 5–10% (including fossil debris). The sediments interfinger with the flank of the mound and are poor in corals, bryozoa, and trilobites, but rich in echinoderm fragments (including calyces of several crinoids, thecae of *Hemicosmites variabilis*, and numerous crinoid ossicles); brachiopods are not uncommon (and include *Sampo* sp., *Glyptorthis?* sp., *Leptaena* sp., *Dolerorthis* sp., a rhynchonellid, *Eospirigerina* and *Lingulella* sp.); trilobites include '*Calymene*' sp. and an illaenid. The preservation of the material and the type of sediment suggests quiet water, probably just below wave base or in a zone of weak currents.

Parasphaeronites n. gen. has only been located in channel fills within the upper Ashgill reef in an unnamed formation (text-figs. 2, 4, 7B) at Ringerike. *Parasphaeronites* occurs in large numbers (hundreds of specimens), closely packed, indicating that they were transported. Their thecae are filled with the same matrix as found in the channel fill, which may indicate a relatively short period of post-mortem transport. *Parasphaeronites* has not been found in the sediments surrounding the reef, and I therefore suggest that they lived either on the reef itself, or in close proximity to it. Their thick thecal walls also support this idea. The associated fauna in the channel fill consists of bryozoa (some of which grew on cystoids), rugose and tabulate corals, stromatoporoids, and algae, all indicative of a shallow water environment; associated echinoderms are *Hemicosmites sculptus* and numerous crinoid columnals and root structures.

CHANGES IN FAUNAL ASSOCIATIONS WITH FACIES, TIME, AND SPACE

The distribution of the echinoderms is closely related to environmental conditions, including the type of substrate, oxygen levels, nutrition, current velocities, and depth. It appears that the diploporites lived in a more restricted range of environments than the rhombiferans, and they may have occupied narrower ecological niches. In the Oslo Region almost all diploporites are restricted to relatively shallow water of four main environmental types: (1) areas with a soft bottom and slow sedimentation rates; (2) areas with a soft bottom but high sedimentation rates; (3) areas with a semiconsolidated bottom; and (4) reef or mud bank environments. The coarseness of the sediment also seems to have been important. Some faunas are restricted to terrigenous sediments, whereas others are found in carbonate sediments. Most stratigraphic sections contain diploporites only in limited intervals. In regressive sections changes in the faunal composition from deeper to more shallow water environments have been observed. Three such examples are described below.

Raudskjær, Asker. The section comprises the upper portion of the Upper Chasmops Shale, the Upper Chasmops Limestone, the Lower Tretaspis Shale, and the Tretaspis Limestone (text-figs. 2, 9A). The Upper Chasmops Shale



TEXT-FIG. 9. Comparison of faunas in the sections at A, Raudskjær, Asker and B, Tønnerud, Hadeland. The Lower Tretaspis Shale and the Gagnum Shale are correlated lithologically, but are considered to be slightly different in time. The differences in lithology and fauna are considered to be related to slight differences in water depth.

contains no diploporites, and is probably a deeper water shale. The size of the clastic grains and faunal diversity increases gradually through the Upper Chasmops Limestone. The upper part is a bioclastic limestone with wave-generated intraformational conglomerates. *Haplosphaeronis* cf. *kiaeri* is present through the Upper Chasmops Limestone, but disappears towards the top of the formation where it is replaced by *Heliocrinites* sp. and *Echinosphaerites* n. sp. of the *grandis* group (text-fig. 9A). The same pattern is found elsewhere in Asker and Bærum (text-fig. 6B), in Langesund and Hadeland, and in Dalarna, Sweden, towards the top of the Kullberg Limestone. No echinoderms with endothecal pore structures occur in this type of environment, possibly because such pore structures were susceptible to clogging by terrigenous sediment. The replacement of *Haplosphaeronis* cf. *kiaeri* by *Heliocrinites* and *Echinosphaerites* is probably related to depth; *Haplosphaeronis* cf. *kiaeri* lived in deeper water. Thus there is a marked upper and lower limit to the distribution of *Haplosphaeronis* at Raudskjær.

Tønnerud, Hadeland. This section comprises the Solvang Formation, the Gagnum Shale, and the Gagnum Limestone (text-figs. 2, 9B). The upper part of the Solvang Formation is a bioclastic limestone containing occasional *Echinosphaerites* of the *grandis* group and *Haplosphaeronis*. Further east, towards the Gagnum farm *Echinosphaerites* is found together with both *Heliocrinites* and *Haplosphaeronis* cf. *kiaeri*. The overlying Gagnum Shale is calcareous (20–60% carbonate) and echinoderms are common. *Echinosphaerites* occurs in the lower part of the section, and *Haplosphaeronis* *kiaeri* is very common from 1 m above the base. *H. kiaeri* is common through the Gagnum Shale and the overlying Gagnum Limestone. The sequence at Tønnerud can be correlated with that at Raudskjær (text-fig. 9; Bruton and Owen 1979). *Haplosphaeronis* is found at Tønnerud in the deepest water sediments. *Echinosphaerites*, and locally *Heliocrinites*, are found in shallow water sediments.

Husbergoya Shale Formation. No more than 2 m thick, this formation can be traced for about 20 km along strike from Oslo to Asker (text-fig. 2). In Oslo terrigenous material dominates, and the fauna includes *Tetreucystis tetrabrachiolata*, *Eucystis langoeiensis*, and '*Heliocrinites balticus*'. Westwards towards what is considered to have been shallower water, *Tetreucystis* and *Eucystis* disappear, but '*Heliocrinites balticus*' continues and an unidentified sphaeronitid cystoid is also present. This change is considered to be depth controlled. A 1° slope of the sea bottom would produce a difference in depth of approximately 25 m between the two major centres of these faunas.

Conclusion. These preliminary studies of echinoderm associations indicate that, although some faunal changes may be referable to differences in water depths, correlations which relate all the echinoderms to depth cannot yet be made. A generalized zonation of the diploporites in the Oslo Region is given in text-fig. 4.

COMPARISON BETWEEN FAUNAS AND COMMENTS ON 'PROVINCIALISM'

It has become popular to talk about faunal provinces of different fossil groups, the echinoderms included. The echinoderms were dispersed as larvae and their dispersal pattern was limited by three major factors: (1) how long the larvae remained free-living before settling; (2) water temperature; and (3) ocean currents. Kesling (1967, p. S136) suggested that the dispersal of cystoids was a slow process. The restricted patterns of distribution of many genera and species suggest that environmental conditions and ecological adaptations were amongst the most important controlling factors in diploporite biogeography. However, several cystoid families had strong geographical preferences at certain times, and this has led to a grouping of the faunas into faunal provinces. Few publications deal with these provinces in terms of plate tectonics (Paul 1976), but it seems that the Oslo Region was in the southern hemisphere during the Ordovician and migrated towards the equator in the upper Ordovician and Silurian.

Estonia, central Sweden, the Oslo Region, and parts of Britain were more or less in the same geographical province (Paul 1976). It has previously been suggested that Britain formed a faunal province separate from that of Norway, Sweden, Estonia, and Ingermanland. Regnéll (1945) described most Swedish diploporites, but three or four extra genera may be present. The Estonian faunas and those of Ingermanland have not been studied in detail since Jaekel (1899), and additional taxa are likely, as suggested by references made to *Haplosphaeronis* and *Sphaeronites* by Männil (1966) and Hecker (1964). The British Diploporita were monographed by Paul (1973); he described several genera not previously recorded from Britain and also pointed out similarities between British and Czechoslovakian mid-European faunas.

Norwegian diploporites are strikingly different from those of other areas, particularly Sweden. This difference is even more evident when rhombiferans are also taken into account. I believe that this reflects differences in environments. The Swedish and Estonian faunas are found mostly in carbonate platform sediments, whereas the Norwegian faunas and the Ashgill faunas of Britain occur in more clastic deposits. In the shallow water clastic environments of the Oslo Region, notably in its northern and south-western margins, the faunas resemble some of those found in similar environments in Estonia and Ingermanland, e.g. *Protocrinites*, *Bockia* (eocrinoid), and *Cystoblastus* (rhombiferan).

The diploporite faunas of Britain, the Oslo Region, central Sweden, Estonia, and Ingermanland are compared in text-fig. 10. The actual number of genera present in the different countries is influenced

DIPLOPORITE GENERA	Bohemia	Belgium	British isles	Norway	Sweden	Estonia Ingermanland
<i>Protocrinites</i>				M. Ord.		L. -M. Ord.
<i>Sphaeronites</i>			U. Ord.	M. Ord.	L. -U. Ord.	M. Ord.
<i>Haplosphaeronis</i>		U. Ord.	U. Ord.	M. -U. Ord.	M. -U. Ord.	M. Ord.
<i>Eucystis</i>	U. Ord. -M. Dev.		U. Ord.	U. Ord.	U. Ord.	
<i>Tetreucystis</i>			U. Ord.	U. Ord.	U. Ord.	
<i>Archaeogocystis</i>	M. Ord.		U. Ord.	U. Ord.		
<i>Glyptosphaerites</i>					M. Ord.	M. Ord.
Total number of genera	5	1	7	8	5	11

TEXT-FIG. 10. Stratigraphical and geographical distribution of non-enigmatic diploporites from Bohemia, Belgium, Britain, Norway, Sweden, and the Baltic states (Estonia and Ingermanland). Totals of the known genera from the different areas give some information about the proportions of enigmatic to non-enigmatic forms.

both by collecting bias and by the extent to which the faunas have been described. Seven to ten genera may have been present in these areas during the Ordovician. It seems that individual species are very restricted even within a single area. This may be partly a preservational feature, reflecting the state of preservation of individual species and the type of environments preserved in different areas at different times, but it also indicates adaptation to particular environments; the appearance or disappearance of species, or even genera, mirror changes in environmental conditions.

There is no clear difference between the British and central and western Baltoscandian Diploporita. On the contrary a gradual shift of the faunas from east to west can be observed. Therefore, environment was the most important factor controlling their distribution.

APPEARANCE, EVOLUTION, AND EXTINCTION

Haplosphaeronis arose in Estonia (early Kukruse, C₁₁) and migrated into the Oslo Region during a transgression in the *multidens* Zone. Different sedimentary environments subsequently developed, to which the diploporites adapted themselves. A regression during the uppermost Caradoc caused a restriction of the diploporites to shallow water environments. By the Ashgill transgression several of the typical Caradoc cystoids had disappeared. These were replaced by new faunal elements which were adapted to shallow water environments. They reached greatest diversity by the maximum of the subsequent Ashgill regression. The base of the Silurian was marked by a transgression of great importance, but no diploporite cystoids seem to have survived into the Silurian in the Oslo Region. Even during several minor transgressions and regressions during the late lower and early upper Silurian no diploporite cystoids appeared. With very few exceptions this pattern is repeated in contemporary deposits elsewhere in the world. Consequently, studies of these changes observed in the Oslo Region may have a wider importance.

It is unknown why the Diploporita periodically disappeared and why there was a faunal shift between the middle and upper Ordovician. Several factors were involved. The Ordovician sediments

in the Oslo Region were deposited in a relatively flat epicontinental sea (Bjørlykke 1974). Most of the terrigenous components were either clay or wind blown quartz of silt fraction. In such environments selection pressure was probably not very great, and faunas were relatively homogeneous over large areas. During the Ashgill, sedimentation rates increased, there was more irregular sedimentation (Bockelie 1978*b*), and the terrigenous components probably increased by a factor of ten. Quartz grain size increased from an average of 35 μm in the middle Ordovician to more than 100 μm (Bjørlykke 1974) in the upper Ordovician. These changes and the development of shallow-water environments may have increased selection pressure and resulted in specialization. Failure to evolve the structures necessary to meet these environmental changes was probably the most important factor in diploporite extinction.

In the upper Ordovician most cystoids have exothecal pores, beneficial in environments with high sedimentation rates and in water with suspended sediment particles. Such areas are common in the uppermost Ordovician in the Oslo Region. Although mudbanks and 'reefs' became more common in the upper Ordovician, the climate was cooler than before; temperature gradients in the upper Ordovician sea would have had a significant effect (Sheehan 1979). Oxygen is more soluble in cold water than in warm water. Cystoids with exothecal pores (Diploporita and some Rhombifera) have many pores and thus a large respiratory surface. They may have thrived in shallow, warmer water with lower oxygen concentration. Most diploporites lacked a stem and were directly attached to objects on the sea floor or to the substrate itself. In times of increased sedimentation, they would easily have been buried.

During the Ordovician the Diploporita may have faced increased competition from other echinoderms, particularly crinoids and rhombiferans. The distribution of ossicles in the Oslo Region shows that the crinoids evolved rapidly and gradually invaded the shallow waters previously occupied by diploporites and rhombiferans. The rhombiferans themselves seem to have been in serious competition with the diploporites.

The cystoids were filter-feeders, so their distribution would depend on the size, composition, and quantity of suspended food. Changes in the plankton might therefore seriously affect cystoid distribution. The size of brachiole facets in both diploporites and rhombiferans increased during the Ordovician (Bockelie 1979*a*), probably induced by change in food supply or increased competition. Larger brachiole facets would have supported longer brachioles and thus allowed an increased food intake.

ANATOMY, TERMINOLOGY, AND FUNCTIONAL MORPHOLOGY

Diploporita are extinct echinoderms having a more or less globular *theca*, a calcareous skeletal body housing the soft tissue, and reproductive organs. The *theca* is composed of thecal plates, arranged randomly or in rings (*circlets*). Some or all of the plates may bear exothecal respiratory pore-structures. *Diplopores*, *humatipores*, and *haplopores* (text-fig. 12) are characteristic of the class.

Four major openings are present: (1) a *peristome*, at the centre of the food-gathering system, which may be covered by a few large or several small cover plates; (2) a *periproct* which in many genera is covered by an anal pyramid of triangular plates; (3) a small, circular *gonopore*; and (4) a slit or sieve-like *hydropore*, indicating the presence of a water vascular system. The *hydropore* and *gonopore* are usually situated close together between the *peristome* and the *periproct* (cf. *Celticystis*, Bockelie 1979*b*). The location of these orifices, and the number and positions of the plates in which they are present, are very important taxonomically.

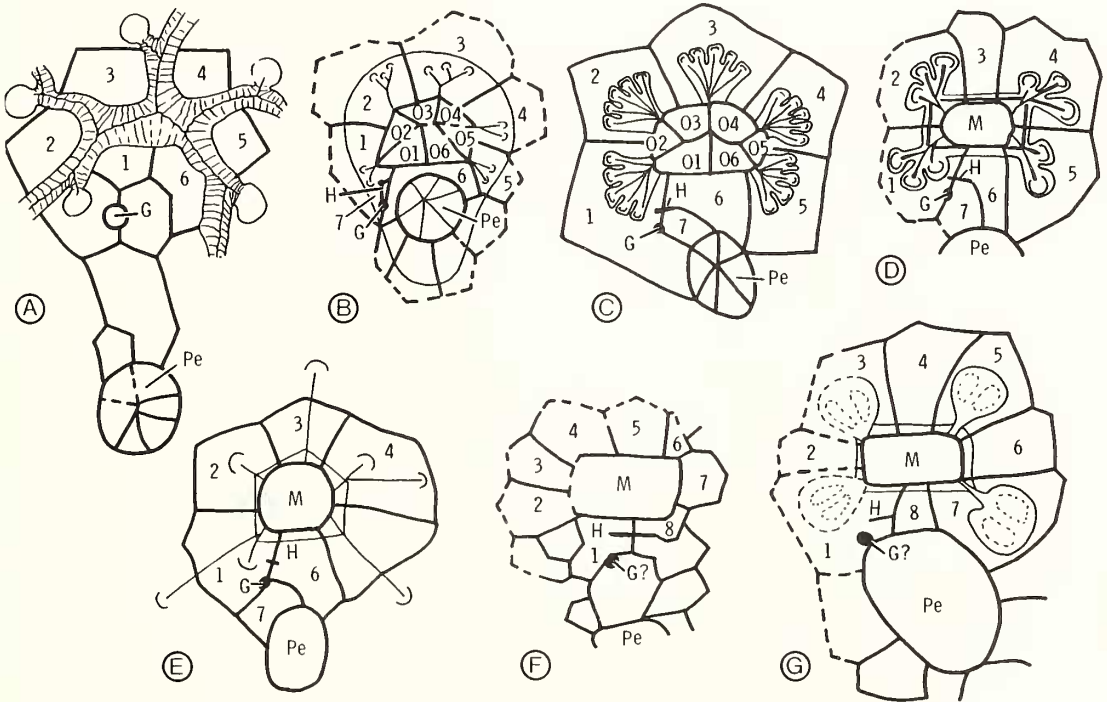
Two to five *ambulacra* extend from the *peristome* and were responsible for food gathering. Food was transported to the mouth along food grooves. *Ambulacral* appendages are very rarely preserved. Only four diploporites with well-preserved appendages are known: *Protocrinites*, *Calix*, and *Glaphocystis* have biserial appendages (Chauvel 1966, 1977); those of *Asteroblastus* are uniserial (Eichwald 1862; see discussion by Jackel 1899, p. 385). The *theca* was attached to the sea bottom by a column of small cylindrical or annular columnals, or by an extension of the basal plates forming a stem-like projection, or directly by its flat base. The *attachment area* can be small or of the same

diameter as the theca itself. Most diploporites were attached, but some may have been free and mobile or even floating.

Most Norwegian Diploporita belong to the family Sphaeronitidae, with one species from the Protocrinitidae; two new genera are erected and placed in a new family, the Parasphaeronitidae. The oro-anal areas of most cystoids are important both for discriminating genera and at family level (Bockelie 1972; Paul 1973). The terminology used in this study is essentially that of Kesling (1967) and Paul (1973). Additional morphological terms are described below.

Major thecal openings

The mouth. Located at the centre of the ambulacral system, the mouth is generally ovate. It is large in the Sphaeronitidae and Parasphaeronitidae n. fam., but relatively small in the Protocrinitidae. It is surrounded by a pentagonal or quadrilateral peristome which in life was covered by six palatals in the Sphaeronitidae, and possibly also in the Parasphaeronitidae. In the Protocrinitidae, ambulacral cover plates continued on to the peristome and covered the mouth (text-fig. 11). The peristome border ('oral laths' of Prokop 1964) of the Sphaeronitidae is present between the mouth and the peristome and on this the food grooves diverge before entering the mouth. In some Sphaeronitidae a complex dendritic pattern of grooves occurs, whereas in others the food grooves continue down into the mouth without branching or diverging (text-figs. 11, 29). The peristome frame is composed of six circum-oral plates in the Protocrinitidae and Sphaeronitidae, and eight plates in the Parasphaeronitidae. The terms *circum-orals* (CO plural COO) and *periorals* were adopted by Paul (1971). Provisionally I refer to the plates which surround the mouth in the Protocrinitidae as circum-orals, without necessarily implying a homology.



TEXT-FIG. 11. Plate configuration of oro-anal area of Norwegian diploporite genera. A, *Protocrinites*. B, *Sphaeronites* (*Peritaphros*). C, *Haplosphaeronis*. D, *Tetreucystis* n. gen. E, *Eucystis*. F, *Parasphaeronites* n. gen. G, *Pachycystis* n. gen. (A, Protocrinitidae. B-E, Sphaeronitidae. F, G, Parasphaeronitidae, n. fam.). M, mouth; G, gonopore; H, hydropore; Pe, periproct.

Food grooves radiate from the oral corners on to the circum-oral plates. In the Sphaeronitidae they may be located on these plates only or continue some distance down the thecal surface. The grooves may or may not branch. Each food groove ends in a small facet, generally less than 1 mm in diameter. The shape and size of individual facets varies at both generic and specific level and may have taxonomic value. In *Protocrinites* long biserial appendages are attached to the facets, and ambulacral cover plates are transformed into specialized brachiolar cover plates on the brachioles (text-fig. 13). The brachioles of *Protocrinites* may be characteristic of most diploporites (see below).

Paul (1973, p. 12) defined an ambulacral formula using the number of ambulacral facets per ambulacrum, starting with ambulacrum I. This number in the Sphaeronitidae has since been related to ontogeny (Bockelie 1978a), but the pattern of distribution over the theca may be typical at family level. In this pattern the number of facets would be the same in radii I and V, slightly less in radii II and III, with the smallest number of facets in radius IV (Bockelie 1978a, p. 36, fig. 5). In some species of *Tetreucystis* (Sphaeronitidae) only one facet per ambulacrum may be present even in adult stages. As reported by Paul (1973, p. 12) no cover plates have been found on the ambulacra of the Sphaeronitidae. In the Protocrinitidae cover plates of two 'generations' occur: large triangular plates along the edges of the ambulacral groove and smaller plates added between (text-fig. 13). Whether similar plates existed in the Sphaeronitidae is unknown. It is clear that food passed along the food grooves of Protocrinitidae and under their cover plates; by analogy, the Sphaeronitidae may have had the same system. Most of the palatals have ambulacral orifices large enough at the peristome for food to have entered beneath them (text-fig. 18). The oral cover plates may have been similar in the Sphaeronitidae and the Parasphaeronitidae.

The anus. Generally circular or oval in outline, it is often as large as or larger than the mouth. When oval, the long axis generally lies at an angle of 60–90° to the lower margin of the peristome. The anus of Sphaeronitidae is present in inter-radius V–I, in contact with circum-oral plates CO5, CO6, CO7, and occasionally CO1 (text-fig. 11). The distance from mouth to anus varies but is generally constant within a genus. In *Sphaeronites* the anus is set close to the mouth; in *Haplosphaeronis* the anus is closer to the mouth than in *Eucystis* and *Tetreucystis* n. gen. but not as close as in *Sphaeronites*; in *Protocrinites* it is separated from the mouth by at least two plate series (text-fig. 11A), while in *Archaegocystis* it is also well removed. The position of the periproct of Parasphaeronitidae may resemble that of the Sphaeronitidae (text-fig. 11), and is not unlike that of *Eucystis* or *Tetreucystis*.

The anus was covered by a pyramid of triangular plates (anals). These plates could open outwards in many genera (text-fig. 26c) because a ledge was present only in the lower half of the periproct (Bockelie 1972; Paul 1973, p. 13).

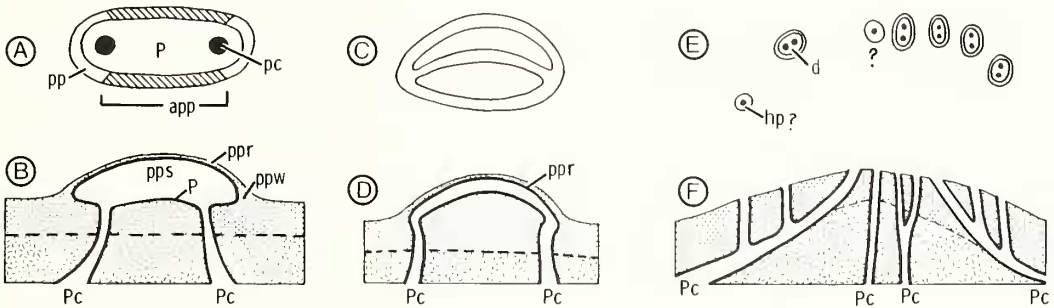
The gonopore. This lies between the peristome and the periproct and is usually slightly left of a line between them. It is a small circular pore generally about 0.5 mm in diameter. Small triangular plates forming a pyramid have been reported in Rhombifera, but have never been found in Norwegian material.

The hydropore. This is normally a narrow slit. In *Protocrinites* a circular opening occurs on top of a small tubercle but it is not known whether this is the hydropore or the gonopore. In the Sphaeronitidae and Parasphaeronitidae a slit is present on top of a ridge. Both the slit-shape and the presence of a ridge would have prevented suspended particles entering; this indicates an inlet rather than an outlet structure (see Paul 1971, pp. 27, 28). A hydropore implies the existence of a water vascular system. Sprinkle (1973) concluded that tube-feet were not present in the brachioles of Blastozoa. Consequently, the water vascular system may rather be related to the pore system (see later discussion). Breimer and Macurda (1972) disagreed with Sprinkle's interpretation and suggested the position of a ring canal in blastoids. Internal and external branches of the water vascular system may be present in both Rhombifera (Paul 1967, p. 234) and Diploporita.

Plates

Individual thecal plates vary in shape, pentagonal or hexagonal being the most common. They are mostly of one generation, i.e. plates formed at an early ontogenetic stage are the only ones involved in skeletal construction (primary plates). Some species and genera possess additional plates formed between others later during ontogeny and termed secondary, tertiary, etc., according to their time of formation. In the Norwegian Diploporita only primary plates occur in *Haplosphaeronis*, *Sphaeronites*, *Archaeogocystis*, and *Eucystis*. Secondary or multigeneration plates occur in *Tetreucystis* n. gen., *Pachycystis* n. gen., *Parasphaeronites* n. gen., and in some indeterminable genera. Both Swedish and British species of *Sphaeronites* and *Eucystis* may have secondary or tertiary thecal plates. Thus, the plate pattern can be quite variable outside the oral area. *Haplosphaeronis* appears to be the only diploporite genus characterized by a constant plate number.

Plate structure. Well-preserved plates of *Parasphaeronites socialis* n. gen., n. sp. (Parasphaeronitidae n. fam.) show two layers of thecal mesh, an inner coarse mesh and an outer fine mesh (text-figs. 12, 33; Pl. 8, figs. 3, 6, 7). Similar observations were made by Paul (1971). However, the coarse layer does not show pillars and laminations as observed in *Archaeogocystis*. The coarse layer has larger trabeculae than the fine layer; the long axes of the trabeculae seem to be orientated at random. In *P. socialis* branched haplopores occur at the boundary between these two layers (text-fig. 12; Pl. 8, figs. 6, 7). Pyrite filling the mesh of *Haplosphaeronis* plates and preservational features of other diploporites also suggest the presence of two layers. Sprinkle (1973) suggested that this pattern is characteristic of all blastozoan echinoderms.



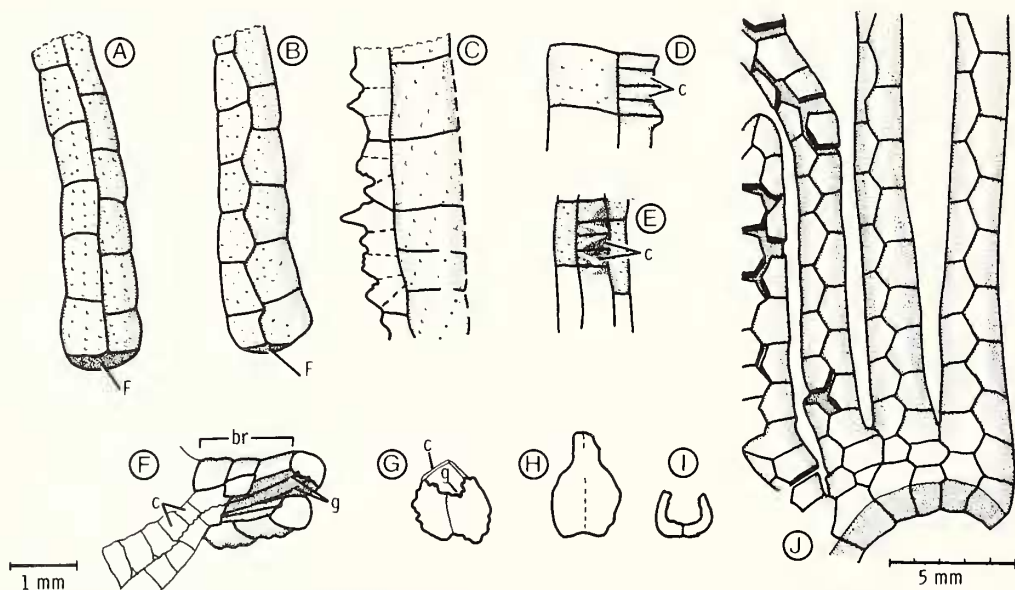
TEXT-FIG. 12. Pore structures in diploporites, showing measurements and terminology. A, C, E, in plan; B, D, F in cross-section. A, B, normal diplopores with or without a calcified periporal roof. C, D, humatipore (not present in Norwegian material). E, F, 'haplopores', simple and complex with unbranched and branched canals. (Originally haplopores were single canals opening in a peripore while diplopores were peripores with two canals. This present structure is much more complex. Notice that simple canals or simply branched canals go through the plate centre, whereas the complex canals lie at an angle to the side of the plate.) The plates are provided with an outer fine mesh of trabeculae (dotted) and an inner coarse mesh structure (irregularly hatched). app, aporal portion of peripore wall; hp, haplopore; P, peripore; Pc, pore canal; pp, poral portion of peripore wall; ppr, periporal roof; pps, periporal space; ppw, peripore wall.

Attachment. The thecae of most Norwegian diploporites were attached by a small or a broad attachment area to any suitable substrate, e.g. cephalopod shells, brachiopods, bryozoans, trilobites, and other cystoids. Some may have been attached to seaweed or soft-bodied animals like ascidians. The basal plates of some sphaeronitid cystoids, especially from Sweden but also from Norway, form a stem-like projection which was either cemented to a firm substrate or may have protruded down into the sediment. *Protocrinites* was the only diploporite in Norway with a stem. The stem was at least 10 mm long and rather complex, its columnals resembling those of shallow-water crinoids. No root structures have been observed.

Food-gathering appendages

Appendages are only very rarely found in diploporites, but facets suggest that they were of different types: some facets are large and indicate attachment for two or more muscular bundles (text-fig. 34A); others are small and hardly show muscle scars or ligament pits at all (e.g. *Haplosphaeronis*). The food-gathering appendages of blastozoans are termed brachioles (see Sprinkle 1973, pp. 12–20). Two major types of brachiole facets occur in the diploporites. Either there is only one facet present in each of the ambulacra even at an adult stage (Holocystitidae, Parasphaeronitidae) or more than one facet is present (most of the Sphaeronitidae, Protocrinitidae). At present only diploporites with the second type of facets have been found with brachioles in place.

Brachioles of Protocrinites. More than a dozen specimens of the Norwegian *Protocrinites rugatus* n. sp. have been found with brachioles in place (text-fig. 13; Pl. 1). The brachioles are biserial, unbranched, reach 15 mm in length, and thus exceed the total length of the theca. In cross-section they are slightly oval or irregular. The two plates that make up the major portion of the brachiole are of approximately equal size when seen in cross-section (text-fig. 13G, H). A set of cover plates is present over the food groove. Four cover plates seem to be attached to every brachiole element (text-fig. 13D, E). In this respect the brachiole resembles the eocrinoid *Gogia longidactylus* (see Sprinkle 1973, text-fig. 10). In *P. rugatus* no traces of nerve canals were found. However, the study was made from decalcified and cast material, and a nerve canal probably was present. In cross-section four minor furrows parallel to the food groove were observed. These grooves could have housed the radial extensions of the water vascular system and other vascular systems. Similar grooves have also



TEXT-FIG. 13. Brachioles of A–H, *Protocrinites rugatus* n. sp. from loose block, Toten, Oslo Region, and I, J, *Calix sedgwicki*. A, PMO 101.133, and B, PMO 101.130, showing dorsal sutures, both biserial but with slight differences in sutural areas. C–H, PMO 101.133, showing c, brachiole in side view with slightly irregular brachiolar cover plates; D, details of brachiolar cover plates (c) in side view; E, brachiolar cover plates from above showing their number and position; F, basal portion of brachiole (br) and brachiolar cover plates, and grooves within the brachiole (g); G, H, cross-sections of brachiole showing shape, brachiolar cover plates (c), and grooves along inside of brachiole (g). I, J, IRScNB 16001 showing I, cross-section of brachiole and J, brachioles showing complex basal portion and biserial appendages (from Chauvel 1977, pl. 1, figs. 5, 6). Scale on left for A–H; scale on right for I, J

been observed in other primitive echinoderms. They may have increased the cross-sectional area of a brachiole and were presumably covered with cilia. These additional furrows alongside the food grooves increased the efficiency and capacity of the brachioles for food transport, and possibly also for food collecting. If no podia were present in the brachioles, the alternative for trapping food particles would have been to possess as many cilia as possible. Similar furrows occur in *Echinospaerites* and *Calix*.

The shape of the brachioles of *P. rugatus* n. sp. suggests that they could stand out almost perpendicular to the theca; they are preserved in a retracted position, slightly bent towards the thecal surface (text-figs. 16, 17; Pl. 1, figs. 1, 6). Even though the animals were buried alive and killed by a rapid influx of sediment, some brachioles were shed. This shows that the contact between the brachioles and their facets cannot have been very strong. If this is typical for other cystoids, it explains the extreme rarity of preserved brachioles, particularly in the Diploporita.

Brachioles of other diploporites. Recent work by Chauvel (1977) has proved the existence of biserial appendages in two Aristocystitidae, *Glaphrocystis globulus* and *Calix sedgwicki*. The brachiole facets of these cystoids are grouped together around the peristome (text-fig. 13i), and partly interconnect to form a rigid brachiole complex before the individual brachioles separate. The brachioles of *C. sedgwicki* are more than 13 cm long, exceeding the length of the theca. Individual brachioles are almost circular in cross-section (text-fig. 13i), and were presumably covered by small plates in life (Chauvel 1977). At the base of and parallel to the food groove Chauvel discovered two minor grooves. A similar complex pattern of the basal portion of the brachioles has been found in a Swedish upper Ordovician aristocystitid (Bockelie, in prep.). On the basis of the observations above, the brachioles of the Aristocystitidae and the Protocrinittidae differ in their basal portions but not in their overall construction. *Asteroblastus* (Asteroblastidae) has uniserial brachioles (see Jaekel 1899, pl. 7, fig. 1) but their details are unknown. Recently a diploporite with *triserial* arms has been found (Parsley 1982).

Brachiole support. Two types of brachiole support seem to be present in cystoids. The Rhombifera and some Diploporita possess *flooring plates*. The ambulacra can be located directly on the thecal plates with brachiole facets (as in most diploporites), while in the majority of Rhombifera and some Diploporita ambulacral flooring plates are found cemented on to the thecal plates. Recently an intermediate situation has been observed in *Celticystis* (Bockelie 1979b) where ambulacral flooring plates occur only in the basal portion of the theca. In the remaining portion of the theca food grooves are developed on 'normal' thecal plates.

Pore structures

All respiratory pore structures of the Diploporita are exothecal, i.e. the body fluid extended from the inside to the outside of the theca and oxygen-carbon dioxide exchange took place through a membrane covering the exothecal pores. In many cystoids the external pores may have been covered by a calcite membrane (most of the Diploporita; see later). Two major types of external pore structures occur in the Diploporita: *humatipores* and *diplopores*. Humatipores are characterized by 'two internal circular pores leading to two or more tangential canals which lie beneath the flat external surface, or in a prominent external tubercle' (Paul 1971). They are confined to the Holocystitidae which are not found in Norway. Diplopores are composed of a simple thecal canal, the tangential portion of which was not normally calcified and probably formed a papula or a podium in life (Paul 1972, p. 5). The normal diplopore shows as two pores, usually paired within a shallow depression (peripore) on the external surface of the theca. In addition to these two major types, *haplopores* have been described by Bather (1900) and Chauvel (1941). A haplopore consists of a single perpendicular canal, apparently ending in a single pore on the thecal surface (see Kesling 1967, p. S89, fig. 33.7). Paul (1972, p. 9) only observed a true haplopore in a plate of *Eucystis* sp. Chauvel (1977) restudied *Calix*, in which haplopores have long been considered characteristic, and observed both normal diplopores and complexly branched or single 'haplopores' in the same individual. He stated that the latter could end in complex sieve-like pores with a peripore. Haplopores have always been considered

to lack a peripore, and Chauvel concluded that they may be regarded as a variety of diplopores rather than a pore structure on their own. It appears therefore that humatipores and diplopores are the only types of external pore-systems in the Diploporita.

Externally the pore-structures of the Diploporita are simple, but this is not the case with the canals leading from the pores through the plates to the thecal interior. Confusion over how the entire pore system was constructed has often been the result. The situation in most genera and species of the Sphaeronitidae is best known where canals lead to the peripores (text-fig. 14), forming part of a circulation system (Paul 1972, fig. 8B). In *Haplosphaeronis* connections of canals may or may not be present (text-fig. 20). *Parasphaeronites* n. gen. shows a complex pattern of canals (text-fig. 12E, F) in which single canals ending in a haplopore(?) go right through the plate close to the plate centre, whereas different types of branched canals occur towards the plate edges (see also Pl. 8, figs. 3, 6, 7). These latter complex canals occasionally end in haplopores, but more usually in diplopores (text-fig. 12E, F). Many or most of the canals of *Parasphaeronites* n. gen. end in diplopores on the thecal surface (Pl. 7, fig. 5), but the details of their connection within the theca are not clear. In *Calix*, the haplopores are located in particular portions of the theca, but their precise distribution is not known; nor is the distribution of these complex pores known in Norwegian material. Haplopores as originally defined may be trans-sutural and thus cross plate boundaries. This is most apparent in *Aristocystites? potens* (Chauvel 1941, p. 68).

Diplopores. These are the most common type of pore structures found in the Diploporita. They are characterized by a pair of canals which open to the exterior in a peripore. Both pores of the peripore are usually on the same plate, but exceptions occur (text-figs. 28, 29, 32). When present, the peripore wall can be divided into *poral* and *aporal* portions (pp, app; text-fig. 12). In *Haplosphaeronis* the aporal portions may develop spines and the poral portions may be almost reduced in some specimens of some species. All diplopores were covered in life by a thin membrane of organic material; some were also covered by a calcitic cupola, occasionally very thin, forming a *calcified roofed diplopore* (text-fig. 12B). Such calcified diplopores can occur in distinct areas (Pl. 5, figs. 2, 4). Inside the diplopore is a *periporal space* (text-fig. 12B). Various *Tetreucystis* n. gen. and *Eucystis* have no pores at thecal plate centres, which might be taken to indicate a lack of pores in extremely young specimens. Alternatively, pores formed at very early stages may later have been resorbed. However, in young individuals respiration could well have taken place directly through their small thin plates (Paul 1972; Bockelie 1979a).

Cystoids have different patterns of diplopore distribution and orientation. The most typical pattern is random, where the long axis of the peripore shows no preferred orientation (text-fig. 31), as in some *Tetreucystis* and *Eucystis* species. Other diploporites have a preferred peripore orientation. In *Tetreucystis kalvoeyensis* n. gen., n. sp. and *Sphaeronites (Peritaphros) pauciscleritatus*, the pore axes radiate from an often slightly elevated plate centre (Pl. 6, fig. 3; Paul and Bockelie 1983). In *Haplosphaeronis* the pore axes are orientated longitudinally in an ad-aboral direction along the radii and horizontally in the interambulacral areas of most species (text-fig. 21). This pattern is unique to *Haplosphaeronis*. *T. kalvoeyensis* has some of its longest pore axes orientated parallel to the oral frame (Pl. 6, fig. 1). These pores may have served a sensory function in addition to the normal respiratory function, becoming specialized and more closely connected with the oral nerve system. Paul (1971) observed numerous pores along the inside of the oral frame of holocystitids and concluded that they served a sensory function. Diplopores are distributed over most of the thecal surface, and are mostly of equal size. However, in a few genera (*Haplosphaeronis*, *Eucystis*, *Tetreucystis*) some diplopores at plate sutures are smaller or deformed.

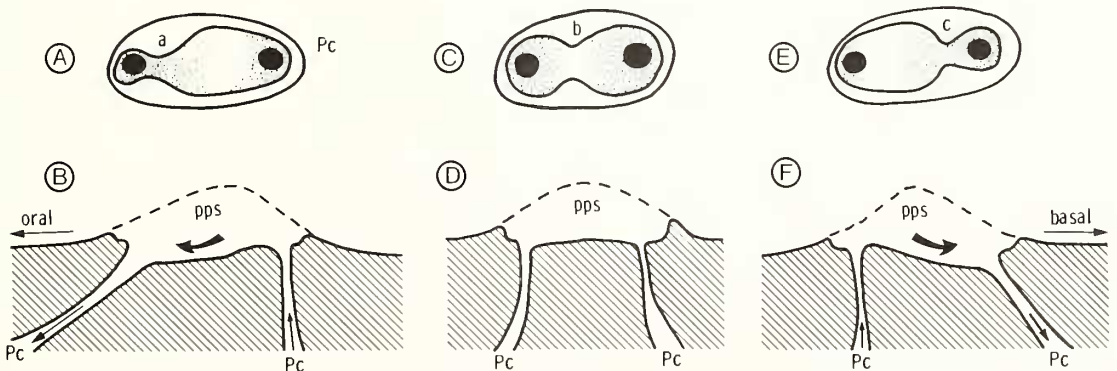
Diplopores may have formed in two ways, either at the plate sutures and gradually migrating towards the plate centre by additional growth (much like that of disjunct pore-rhombs) or alternatively, and most likely, by resorption of the plate. Many diplopores in *Haplosphaeronis* near the plate sutures are smaller than those closer to the plate centre (Pl. 3, figs. 3, 5). These may be in the position of formation, and thus resorption would have continued until maximum size of the diplopore was reached. Many individuals of *H. kiaeri* have pores at plate sutures, but apparently lack

pores closer to the plate centre (Pl. 5, figs. 2, 4). Instead, there are small knobs or 'ornament' randomly distributed on these plates which, when ground down, prove to be deformed diplopores with an originally calcified cupola.

The number and position of diplopores varies between individuals and some plates have more than others. The highest number is present in the circum-oral plates of the Sphaeronitidae. This upper portion of the theca is considered to have been in the zone of the highest water speeds passing over the theca, and it therefore possibly had the highest respiratory potential (Bockelie 1979b).

Covered diplopores. Diplopores are considered by many authors to have been covered in life by soft tissue. However, the presence of peripores covered by a calcitic cupola has been reported from many different genera and species of Diploporita. This has been explained as accidental preservation, or as being related to the sealing of parts of the respiratory system to prevent toxic gases from entering. Norwegian diploporites are often found with roofed diplopores in distinct areas, often towards the base or the oral area. Occasionally most of the theca is covered by roofed diplopores (Pl. 5, fig. 4). In addition to the roofed diplopores there are several pores that do not have a calcitic cupola, and probably never had one in the living state. This is particularly obvious in *H. kiaeri* (Pl. 5, fig. 3). The presence or absence of calcite-roofed diplopores is partly a preservational feature. Extremely well-preserved material often has the roof preserved, as in *H. kiaeri* (Pl. 5, figs. 2, 4) and *Protocrinites rugatus* n. sp. (Pl. 1, figs. 1, 3, 5, 8). However, both these species were usually buried rapidly. In cases where burial was slower the roofed diplopores may have become abraded. Similar preservation on holocystitids confirms this. Even specimens of *Sphaeronites* (*S.*) *pomum* from Öland, Sweden, are occasionally found with extremely thin calcite roofs preserved.

The presence of calcite-roofed diplopores had several advantages. For the animal's internal flow system it would have helped keep a constant volume under the periporal roof. Previous suggestions that it would also have prevented toxic gases from entering the animals attached to the sea bottom may not be correct if the calcified diplopores were porous. (*P. rugatus* is provided with a stem and also has covered diplopores.) A third explanation implies protection from predation of soft tissue or papulae over the diplopores. There was no protection, such as spines, around most peripores (with the exception of *S. (S.) pomum* and some specimens of *H. kiaeri*). The formation of a calcite cupola would have reduced predation of soft tissue which might otherwise have been fatal to the animal. Covered diplopores are more common in the upper Ordovician and Silurian diploporites than in the lower and middle Ordovician forms.



TEXT-FIG. 14. Pore-structures of *Haplosphaeronis kiaeri*; A, C, E in plan, showing thickenings and spine development (a, b, c) on the peripore wall and B, D, F in cross-section showing angle of canals through the plates in different parts of the theca. B, near oral area, with oxygenated body fluid moving towards oral portion. D, midway down theca (note symmetrical arrangement of the two canals). F, near base with oxygenated body fluid moving towards basal portion. Arrows indicate direction of flow of body fluid inside canals. a, b, c, thickened parts of aporal portions of periporal rim; pps, periporal space; pc, canals (note they do not have the same thickness throughout the plate).

Diplopores are less efficient respiratory structures than endothelial dichopores and, consequently, more diplopores are needed to match the oxygen-carbon dioxide exchange rates achieved by cystoids with endothelial structures. A calcitic cupola would have reduced the efficiency of respiration only slightly, possibly as little as 10–15% (see Paul 1978).

Circulation in diplopores. In *Haplosphaeronis* the form of peripores differs according to their position on the theca (text-fig. 14). In the oral area, the adoral canal of any diplopore slopes towards the oral pole at an angle of 20–30° while the other canal is almost perpendicular to the surface. I suggest that oxygenated body fluid passed down under the oral area in this part of the theca (text-fig. 14B). Similar but reversed patterns have been found in the basal portion of the theca. Here oxygenated body fluid passed down into the basal portion of the theca (text-fig. 14E). Canals between these two extreme positions show variable angles, according to the location of the diplopore on the thecal surface. Peripore distribution over the theca of *Haplosphaeronis* suggests a flow direction of body fluids counteracting that of the external water current pattern around the theca (see Paul 1972). A similar pattern has also been suggested for *Hemicosmites* (Bockelie 1979a). The complex pattern of pore systems found in *Parasphaeronites* n. gen. cannot be evaluated at present in terms of thecal flow pattern. However, there appears to be a radiating pattern similar to that found in some species of *Tetreucystis* n. gen. and *Sphaeronites*.

Connections of canals inside the plates. In the aristocystitids branched haplopores have been known since the work of Barrande (1887). In the Sphaeronitidae Paul (1972, fig. 8A, B) illustrated the two possible models for peripore connections and argued strongly for the Y-shaped canals having fed separate peripores. He showed how unlikely it was that the Y-shaped canal fed the same peripore, because this would have created a mixing of oxygenated and deoxygenated currents. In some of the Norwegian species of *Haplosphaeronis* the canals are filled with tiny pyrite crystals and terrigenous mud. Careful dissolving of the thecal plates reveals canals going through the plate connected to canals of adjacent peripores, confirming Paul's fig. 8B (text-fig. 12).

Connections of canals of adjacent peripores occur frequently in *H. kiaeri* (text-fig. 20r) and have also been observed in *Eucystis globula* Paul (SM A74861) and *Parasphaeronites socialis* n. gen., n. sp. (text-fig. 12F; Pl. 8, figs. 3, 6, 7). These connections indicate the presence of an internal circulation system. Mapping the entire pattern of pore connections over the theca is exceedingly difficult and time-consuming and requires exceptional preservation. Some idea of the pattern can be obtained from *Haplosphaeronis* (text-fig. 20r). In this genus the diplopores are arranged parallel to the thecal axis over most of the animal, with the peripores radiating from each of the oral corners. Connections have only been observed between two adjacent diplopores at a time (text-fig. 20G). Pore canals merge in such a way that one gets the impression of a dichotomously branched pattern (text-fig. 20t).

Diplopores may have been produced by coelomic evaginations, which could have led to a random distribution of peripore connections. The radiating pattern observed in some *Tetreucystis* species may be related to such a system. On the other hand, peripore connections such as those found in *Haplosphaeronis* may indicate a more intricate and well linked flow system similar to the tube-foot connections of echinoids. These differences in pore systems have considerable taxonomic implications. The second explanation accounts for the presence of a hydropore, but the first does not. Which of the two alternatives is correct cannot be ascertained at present, but the fact that the diplopores appear interconnected suggests the presence of a complex connective hydrovascular system. The hydropore, which indicates the presence of a water vascular system, could thus be connected to the pore system, rather than to a system of tube-feet located in the brachioles. Sprinkle (1973, p. 21) suggested the absence of tube-feet in blastozoan brachioles. Paul (1967) suggested that both internal and external branches of a water vascular system might have occurred in the rhombiferans. This is also possible in the diploporites.

Internal morphology

Relatively little is known of the internal morphology of cystoids. Observations include mesenteria of *Echinospaerites* (Jaekel 1899; Regnéll 1945) and the intestine of *Caryocrinites* (Rhombifera)

described by Jaekel (1918). Sinclair (1948) and Regnéll (1951) also made internal observations. Termier and Termier (1959) suggested the presence of various oral ring canals. Internal features are known from the Oslo Region's echinoderms, particularly *Haplosphaeronis*.

Internal spine and basal pits. Many specimens of *Haplosphaeronis* have a hollow internal spine like that described by Paul (1973, p. 21, text-fig. 12) from *Sphaeronites* (*Peritaphros*) and *Haplosphaeronis*. This conical spine is well preserved in silicified specimens of *H. kiaeri* (text-fig. 22; Pl. 4, figs. 8, 9). It extends from the base for approximately one-third of the thecal height. It is a continuation of the inside of the basal plates but the plates themselves seem to have amalgamated at the base of the spine. However, one suture is present alongside the spine in some specimens. It may be open for some distance and is internally strengthened by calcite. A hole is present at the adoral end of the spine, indicating that it was hollow. An internal spine has been located in several genera of the Sphaeronitidae (*Haplosphaeronis*, *Sphaeronites* (*Peritaphros*), *Tetrecystis* but not as yet in *Eucystis* or *Sphaeronites* (*Sphaeronites*): Paul 1973, p. 41). An internal spine may be present in the Aristocystitidae (*Calix* and *Pachycalix*, Termier and Termier 1959), but it has not been recorded in other diploporites.

The functional significance of the internal spine is unknown. It shows similarities to the chambered organ of some crinoids, notably *Neocrinus decorus* as described by Reichensperger (1905) and *Eugeniocrinites caryophylatus* (see Ubaghs 1978, p. T192, fig. 162.1), and may have served a similar function. Regardless of its origin, the spine seems to have grown continuously during the animal's life, and must have served some function in both young and adult specimens.

Around the base of the spine and in contact with the inside of the basal portion of the basal plates lie seven cavities penetrating into the thecal plates of *Haplosphaeronis*, one at each of the plate sutures. In addition, a variable number of smaller cavities is found between the seven larger ones (text-fig. 22; Pl. 3, fig. 11). All cavities are present at approximately the same level and form conical depressions. Several dozen specimens with this type of structure preserved have been found. In some pyritized specimens (text-fig. 22D), a small depression surrounding the base of the spine is located between the grooves on the inside of the thecal wall and the internal spine. This depression may have housed an ectoneural nerve ring, and the grooves on the inside of the thecal wall may have been locations for side canals (text-fig. 22). The grooves on the inside of the thecal wall were not attachment areas for muscles or coeloms, since such attachment areas usually take the shape of bosses or evaginations rather than invaginations.

An ectoneural nerve ring is known in many fossil and recent crinoids, it being the main nerve system for innervation of arms and stem (Ubaghs 1978, p. T190), but there are great constructional differences between the arms of crinoids and the brachioles of cystoids (Ubaghs 1978, p. T133). Even so, an ectoneural nerve system was probably present around the base of *Haplosphaeronis*. Certain internal features in the basal portions of the thecae of the diploporite *Celticystis* (Bockelie 1979b) and in the rhombiferan *Hemicosmites* (Bockelie 1979a) may also represent traces of an ectoneural nerve ring. No traces of nerve canals leading from the base towards the oral area have been found.

Structures associated with the oral area. In sagittal view some specimens of *Haplosphaeronis kiaeri* have cavities within the plate just under the ambulacra (text-fig. 23B; Pl. 4, fig. 4). These may be parts of a circum-oral structure, but as yet too few specimens have been studied to confirm this. Steinkerns of decalcified specimens show an irregular underside of the theca just below the circum-oral area (Pl. 4, fig. 8) which may indicate that circum-oral structures were also present within the soft tissue below the skeleton. Silicified specimens of *H. kiaeri* show five lobes (0.4 mm thick) just under the ambulacral area (text-fig. 23A; Pl. 4, figs. 3, 5). Even though details of the lobes are not adequate, there is no doubt that at least one penta-lobate ring canal was present in the soft tissue of the circum-oral area. Similar structures have been suggested for other diploporites (Termier and Termier 1959; Bockelie 1979b). The reconstruction of *Pachycalix* (Aristocystiidae) is particularly interesting in this respect (Termier and Termier 1959; Kesling 1967, p. S245, fig. 143.2a) in which the presence of three ring canals was suggested. Whether or not the ring canal observed in *H. kiaeri* is associated with the water vascular system is not known.

Other internal structures. When decalcified, most specimens of *Haplosphaeronis* show traces of a 'gonoduct' and a 'stone canal' which are typical of other cystoids. These canals pass through the plate on the left side of the theca. The close proximity of gonopore and hydropore makes it difficult to decide which canal is the gonoduct and which the stone canal. However, in PMO 89996 (Pl. 4, fig. 2) the gonoduct and the stone canal are not connected, the former going straight down into the theca at the left side of the periproct. The hydropore, which at the thecal surface is a slit on the top of an elongated mound, becomes wider as it goes through the plate. When through the plate, the stone canal bends to the right and is located in a groove on the inside of the theca between the peristome and the periproct. The stone canal, which here has a circular cross-section, continues to the right and bends towards radius V where it is located just under the ambulacrum. At this position it becomes more flattened in cross-section and stops at the plate suture CO4:CO5. It is possible that the stone canal is connected to the penta-lobate ring canal just described. If this is the case, then it may indicate a well-developed ring canal of the water vascular system. Sprinkle (1973, pp. 21-27) discussed the possibility that tube-feet of the water vascular system were located in the brachioles but could find no support for such an assumption. I agree with Sprinkle, and prefer to relate the water vascular system to the blastozoan pore system. However, no fossil material exists to prove this assertion.

Occasionally thin films of pyrite can be seen attached to the thecal interior which follow a pattern not unlike that observed in *Echinospaerites* by Jaekel (1899). These may represent remains of a mesenterium, but the number of specimens involved is small.

MORPHOLOGICAL LINEAGES IN THE DIPLOPORITA

Evolutionary trends must fulfill two criteria: (1) they must involve closely related species (preferably within one family); (2) they must be time dependent. Even if these two criteria are fulfilled, one is often left with just the two end members, i.e. an early species and a late species. Two species of a genus might be quite different, not only because they occur at different stratigraphical levels, and thus may represent a phylogenetic lineage, but also perhaps equally important is the fact that they may occur in two different environments. Morphological lineages can be observed in some diploporite cystoids, but often they can only be inferred. In many cases the importance of morphological lineages in phylogenetic evolution cannot be evaluated. *Haplosphaeronis* illustrates some of the problems involved. Specimens occurring in shales are usually smaller than those in nodular limestones. The smaller specimens may be adults in the shale populations, whereas individuals of similar size occurring in nodular limestones may not have reached maturity. The number of brachiole facets of this genus increased during ontogeny (Bockelie 1978a), but to demonstrate this required large collections. One might have concluded that the number of brachiole facets changed with time, rather than ontogeny. Some morphological lineages, or what appear to be such, are discussed below.

Thecal plates. The number of thecal plates may increase or decrease with time in some genera. In *Sphaeronites* a reduction in plate number occurs from early to late Ordovician (Paul and Bockelie 1983). In other genera this has not been studied to the same extent. There is a general tendency towards reduction in the number of plates in many cystoids (see also Bockelie 1979b). A reduction takes place when the number of plates present in young individuals is retained to the adult stage. Enlargement of the theca then occurs by growth of individual plates only and not by the addition of secondary or tertiary generation plates. In this respect, *Haplosphaeronis* is an advanced genus because the number of thecal plates remains constant in young and adult specimens. *Celticystis* (Bockelie 1979b) and *Protocrinites* (text-fig. 16) add new thecal plates in particular 'growth zones'. Plate reduction with time is also marked in many primitive echinoderms. The change from a large number of irregularly arranged calyx plates to a much smaller number usually showing good pentamerous symmetry appears to have occurred independently in several groups of both Blastozoa and Crinozoa. In species with a large number of thecal plates, individuals seldom have the same arrangement of

calyx plates (see *Protocrinites*, text-figs. 16, 17). In species with a total plate number between fourteen and thirty-five the plates are arranged in symmetrical patterns, and most individuals of the same species have their plates arranged in the same manner.

Ambulacra. In the diploporite cystoids most genera and species have five ambulacra, but genera with two, three, and four exist. In the Sphaeronitidae genera with four ambulacra have radius III reduced (*Tetreucystis* n. gen., *Diplosphaeronis*). In other families genera and species with four ambulacra exist (*Trematocystis*, Holocystidae; *Parasphaeronites* n. gen. and *Pachycystis* n. gen., Parasphaeronitidae). These genera and species are parallel lineages in which radius III is reduced.

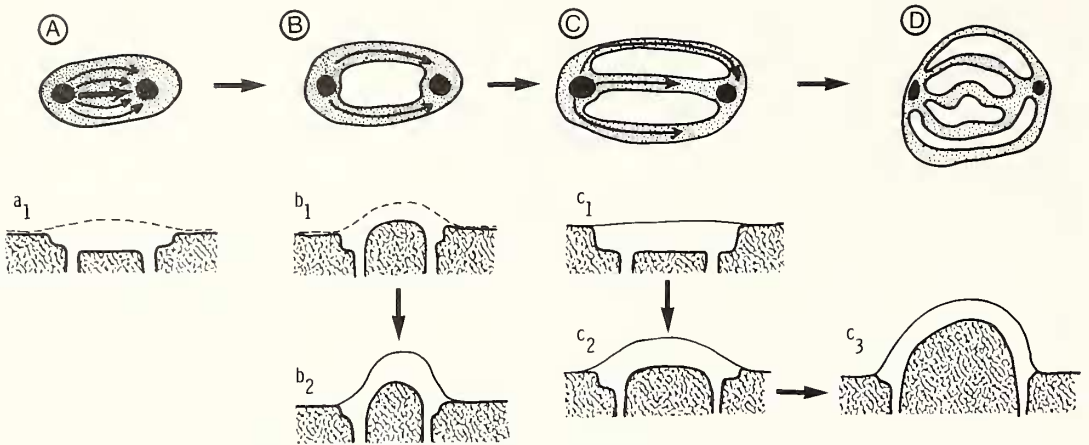
In *Eucystis* the number of brachiole facets and their position over the theca differs with time. Ordovician species may have from one to four facets close to the mouth. During the upper Ordovician and particularly in the Devonian the number of facets increased and the food grooves migrated down over the sides of the theca (Bockelie 1978a) resulting in an increased area for food collecting. An increase in the number of brachiole facets also occurred in *Tetreucystis* n. gen. and in *Haplosphaeronis*, but in complex ways. As mentioned previously, the highest number of brachiole facets in *Haplosphaeronis* is found in Britain, whereas contemporaneous species both in Norway and Sweden have fewer facets. In *Tetreucystis* n. gen., British species have few brachiole facets, Norwegian species have an intermediate number, and contemporary Swedish species have the highest number. What might appear to be a phylogenetic trend may in fact have been related to contemporary ecological conditions.

In *Haplosphaeronis* the brachiole facets may have different shapes (text-fig. 19). In an early species, *H. bratterudensis* n. sp., the first formed facets (Bockelie 1978a) usually have a rounded outline, whereas later ones are angular or almost square. During the late middle Ordovician and the upper Ordovician all facets became rounded in outline (text-fig. 19c, d). A general impression is that the facets also became larger during that same time span. Similar studies do not exist for other genera and species, and thus it is difficult to evaluate how common such a morphological trend may be. Early Ashgill species of *Tetreucystis* n. gen. generally have smaller brachiole facets than later Ashgill forms, and species with only one facet in each ambulacrum have larger facets than those with more. However, one facet in each ambulacrum is primitive while the presence of several facets is a derived character, as can be demonstrated in several genera and species (see also Bockelie 1978a). In *Protocrinites* young individuals have few facets, whereas older individuals have more (text-figs. 16, 17). In *Celticystis* new facets are added constantly (Bockelie 1979b).

Pore structures. The pore structures underwent changes throughout their history. A study of diplopores and their changes with time has been undertaken in *Sphaeronites* (Paul and Bockelie 1983) where there is an increase in the size of the pores and a corresponding decrease in their number. In *Haplosphaeronis* the width of the peripores decreased during the Ordovician (text-fig. 25). One of the most marked changes found in the pores of *Haplosphaeronis* is the elevation of the periporal floor from a position below the thecal surface in *H. bratterudensis* (early Caradoc) to a position level with or above the thecal surface in *H. kiaeri* (upper Ordovician). Together with this trend is an increase in the aporal portion of the peripore to form a spine-like peripore rim (Pl. 5, fig. 3).

The formation of a calcitic cupola can be observed in several genera and species throughout the Ordovician and appears to be a parallel development. No calcitic cupola is present in *H. bratterudensis* but it is very common in *H. kiaeri* and has also been found in British Ashgill species and some populations of the Swedish upper Ordovician *H. oblonga*. A calcitic cupola seems to accompany an elevation of the peripore from the thecal surface. Thus in most diploporites where the peripores are present on 'pustules', they have a calcitic cupola.

Haplopores have been considered the simplest type of pore structure but this may not be correct. The internal connections of pore structures are not well known so we do not know the course of canals through the plates in many diploporites. However, the external peripore in many of the early Ordovician species is sunk below the thecal surface and may have a weakly developed periporal rim and represent a simple stage (text-fig. 15A). During the middle Ordovician the periporal floor became elevated in *Haplosphaeronis* and *Sphaeronites* (*Peritaphros*) (text-fig. 15B). By a further elevation of



TEXT-FIG. 15. Morphological series of changes in pore structures. A, simple, open pores. B, formation of elevated periporal floor and slight diversion of body fluids into two separate currents. C, tri-partition of body fluids in tangential canals. D, more complex pattern of tangential canal formation. a, b, c, cross-sections of pore structures within the general form patterns. a₁, simple peripores in *Glyptosphaerites* and early *Haplosphaerionites* species. b₁, b₂, development of an elevated periporal floor, typical of *Sphaerionites* (*Sphaerionites*) and *S. (Peritaphros)* species (a broken line indicates non-calcified periporal roof; a continuous line indicates calcified periporal roof). c₁–c₃, stages of development in Holocystitidae and Aristocystitidae in which calcified cupola is commonly present (note elevation of the periporal floor to form knobs with large surface areas).

the periporal floor a calcitic cupola was formed over the peripore, probably to keep a constant volume within the pore space or to protect these vital structures from predation. Most diploporite pore structures did not evolve beyond this stage (text-fig. 15B). In some genera the periporal floor divided, thus separating the currents of body fluids into the two flow directions seen in *S. (Peritaphros)*, or into three or more such currents (text-fig. 15C, D). In extreme cases the cupola became strongly elevated (text-fig. 15C₃). The trend towards the formation of humatipores in the Holocystitidae and a pustule-like cupola may be regarded as stages in the evolution of a better protected respiratory system.

It seems that the changes with time found in the respiratory pore structures are most important for the class Diploporita. It is probably likely that morphological trends of the brachioles are equally important (see above), but without suitable material, this is speculation.

SYSTEMATIC PALAEOLOGY

Phylum ECHINODERMATA Bruguière, 1789

Subphylum BLASTOZOA Sprinkle, 1973

Class DIPLOPORITA Müller, 1854

Diagnosis. Thecal pores developed as units mostly confined to single plates, typically in the form of diplopores, but present in some as haplopores or humatipores. Lower Ordovician (Tremadoc)–middle Devonian.

Remarks. Brachioles of the Diploporita do not differ from those of most Rhombifera or most Eocrinoidea. Paul (1968a, p. 594; 1968b, pp. 726, 727) proposed that the name Cystoidea be dropped and that the Rhombifera and Diploporita be given class rank. This was accepted by Sprinkle (1973, p. 170) and is also accepted here. Sprinkle (1973) discussed whether or not the Diploporita should be

assigned to the Blastozoa. The discovery of biserial appendages in several genera of the Diploporita strengthens the assumption that this class belongs to the Blastozoa (see also discussion by Chauvel 1977, p. 317). The diagnosis given above differs to some extent from that of Ubaghs (1978, p. T362) who did not recognize the subphylum Blastozoa. However, this present study shows that the Diploporita have the type of plate growth which is characteristic of other Blastozoa.

The Diploporita appear to be a fairly homogeneous group of primitive echinoderms, all having exothecal pore systems. The Diploporita seem to form a natural group but this is not so with the Rhombifera. As suggested by Paul (1972) and discussed by Sprinkle (1973, p. 170), the Rhombifera consist of two distinct groups of cystoids, one with endothecal structures and one with exothecal pore structures. It is difficult to see how one could have given rise to the other.

Superfamily GLYPTOSPHAERITIDA Bernard, 1895

Diagnosis. Diploporite cystoids. Ambulacra radial, extending over theca, with alternating lateral branches (single or in groups) leading to brachiole facets; in many genera, ambulacra bordered by alternating 'adambulacrals' on which facets are located. Diplopores invariably present on ambulacra-bearing plates, in some forms also in the interambulacral areas. Most with column, a few moulting column as adults.

Family PROTOCRINITIDAE Bather, 1899

Diagnosis. Diplopores on ambulacral and interambulacral plates alike. Ambulacra extending radially from peristome, with short branches to brachiole facets more or less alternating. Ambulacral cover plates continue on to the oral area where they become oral cover plates. Thecal plates bearing rather regularly alternating ambulacral plates comprising so-called 'adambulacrals'. Brachioles biserial.

Remarks. Genera of the family Protocrinitidae differ considerably from those of the Glyptosphaeritidae. These two families are grouped together with the Dactylocystidae and the Gomphocystidae in the superfamily Glyptosphaeritida by Kesling (1967). *Glyptosphaerites*, the only representative of the Glyptosphaeritidae, has an oral cover resembling that of sphaeronitids but differs considerably from that of all other families. Thus the Glyptosphaeritidae may be more closely related to the Sphaeronitidae than to other families. The Protocrinitidae and the Dactylocystidae seem to form a natural unit, quite different from the other two families of the superfamily. A subdivision of the Glyptosphaeritida may prove necessary in the future.

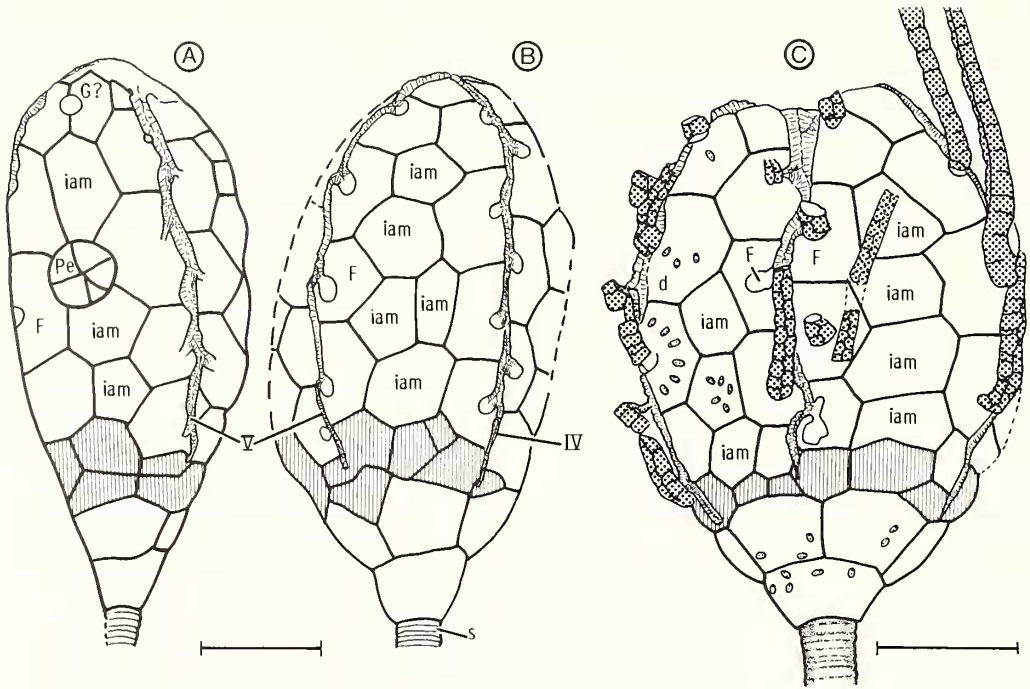
Genus *Protocrinites* Eichwald, 1840

Type species. *Protocrinites oviformis* Eichwald, 1840, p. 185, from Põõsaspea (Spitham), Estonia, Jõhvi Stage (DI), middle Ordovician.

Diagnosis. A genus of Protocrinitidae with triangular peristome surrounded by six circum-oral plates; five ambulacra, each containing dichotomously branched food grooves, terminating in a facet on each thecal plate, or continuing on to biserial appendages when present; ambulacra confined to specialized adambulacral with one facet on each adambulacral plate; adambulacral plates separated transversely by one or occasionally two interambulacral plate series.

Remarks. This diagnosis differs from that given by Kesling (1967) in several respects, partly because the number and distribution of circum-oral plates may be an important character of most cystoids. In the Sphaeronitidae, this is certainly the case. Jaekel (1899) regarded *Fungocystites* Barrande as a synonym of *Protocrinites* but later (1918) accepted the two as separate genera.

Description. The thecae are apple or egg-shaped. *P. rugatus* sp. nov. is small with thecal diameter 15 mm, whereas *P. oviformis* and some *P. fragum* are 50 mm. Five ambulacra, each containing dichotomously branched food grooves, extend from the mouth. The ambulacra do not reach down to the basal plates, but stop on the third



TEXT-FIG. 16. *Protocrinites rugatus* n. sp. Adult thecae. A, B, PMO 101.132, different views showing radii IV and V and position of gonopore (G?) and periproct (Pe) in relation to ambulacrals and interambulacrals (iam). Notice that ambulacral channels end in the growth zone (vertically ruled). C, PMO 101.138, showing biserial brachioles (dotted), brachiole facets (F) and some diplopores radially arranged on the ambulacral plates. s, proximal portion of the stem. Scale bar, 5 mm.

plate series up from the basals (text-fig. 16; Pl. 1, fig. 8). New ambulacral facets were added to the distal portions of the ambulacral furrows throughout life. The number of facets per ambulacrum increased from two in young specimens to nine in larger ones. The ambulacral furrows are covered by small cover plates arranged in an intricate pattern (text-fig. 17B; Pl. 1, fig. 3). A biserial appendage up to 15 mm long extended from each of the ambulacral facets. The appendages are as long as the theca itself (text-fig. 16; Pl. 1, figs. 1, 4).

The basals of *Protocrinites* vary in number. According to Volborth (1846) the number in *P. oviformis* can vary between three and six. In *P. rugatus* sp. nov. all the basals are fused into one unit. Diplopores are present all over the theca. In Norwegian species it appears that most or all the pores were covered in life, either by an organic membrane or, most likely, by a thin calcitic membrane. This membrane was easily abraded, leaving the pores open in specimens exposed for some time before final burial. The pores on adambulacral plates tend to be orientated with their long axes perpendicular to the ambulacrum, as observed by Jaekel (1899, pl. 5, fig. 6a).

The periproct is situated laterally on the theca, but its position may vary (Jaekel 1899). In general, two or three plates separate the periproct from the mouth (text-fig. 16A). The periproct is circular and covered by a pyramid of five or six triangular plates. Both a gonopore and a hydropore have been reported on *P. fragum* (Yakovlev 1940, fig. 1). In the Norwegian material a tubercle may be present either on the CO5:CO6 suture (PMO 101.138 and 101.136) or on the left sutural area of the upper interambulacral plate between radii V and I (PMO 101.132 and 101.130, text-figs. 16A, 17A). This tubercle may represent either the gonopore or the hydropore. Eichwald (1840) and Jaekel (1899, pl. 5, fig. 3) also observed a tubercle on CO6.

Attachment: some species had a stem, and one was certainly present in *P. yakovlevi* (Hecker 1964, pl. 5, fig. 5) and *P. rugatus* sp. nov. (Pl. 1, figs. 1, 2). In *P. yakovlevi* an attachment disc was present. Discs may also have been present in other species. In *P. fragum* no stem has been observed. Jaekel (1899, p. 430) suggested that this species lacked a stem in adult stages. *P. oviformis* is known to have had a stem when young, but it was lost in adults (Volborth 1846).

Growth: the growth pattern of *Protocrinites* was previously unknown. In the Norwegian material, however, one small specimen occurs together with larger ones. The plate configurations and food-gathering appendages give some indication of the growth pattern. In the smallest specimen (5 mm high, 5 mm in diameter) only two brachioles are present in each of the ambulacra, whereas in larger specimens seven to nine brachioles are present per ambulacrum depending upon the size of the theca. This indicates that new appendages were added through life. The length of the brachioles also seems to have been related to thecal size. However, few specimens have complete brachioles. The ratio of brachiole length to thecal size is greater in smaller specimens than in larger ones (text-figs. 16, 17c). This may indicate that the small specimens could obtain proportionally larger quantities of food for rapid growth.

New plates were added; the important growth zones seem to be in the third plate series from the base of the theca (text-fig. 16). The plates in this zone do not appear to be differentiated, whereas those immediately adorally do (text-fig. 16). Growth in this part of the theca did not interfere with food-gathering, nor with the stem and its attachment to the basals. The theca also grew by normal accretionary growth of individual thecal plates (Sprinkle 1973). The addition of new thecal elements in this growth band thus comprises: (1) addition of new thecal plates, including adambulacrals and interambulacrals; (2) continued extension of ambulacral furrows and ambulacral cover plates; (3) formation of new brachiole facets; and (4) possibly formation of new diplopores. Diplopores also appear to have been formed by resorption of skeletal material wherever a new pore was needed, and their formation may have been less important than the formation of other thecal elements in the growth zone.

Palaeoecology. The stem-bearing Norwegian species lived on a muddy bottom in an unstable sedimentary environment. *P. oviformis* is not uncommon in the Jõhvi stage in Estonia and Russia but little is known concerning its palaeoecology. According to Jaekel (1899, p. 430) *P. fragum* was heavy, stemless, and probably free-living on the sea bottom. Its size and shape suggested to him slow movement, if any. The somewhat flattened shape of the animal would have prevented it from sinking into the soft sediment on which it lived. *P. yakovlevi* was attached by a stem and a disc, but nothing is known about the environment in which it lived.

Regional distribution. Norway, Estonia, Leningrad district of Russia (Jaekel 1899; Hecker and Hecker 1957), Thüringen, Germany (Freyberg 1923), Burma, India (Bather 1906).

Stratigraphical range. Arenig–Caradoc.

Protocrinites rugatus n. sp.

Plate 1, figs. 1–8; text-figs. 13A–H, 16, 17

Diagnosis. A species of *Protocrinites* with a strongly rugose plate surface and stem present. Interambulacral rows may contain two interambulacral plates in interradius IV–V. Basals fused to form a solid basal cup for stem attachment.

Holotype. PMO 101.138 preserved as an external mould.

Horizon and locality. Coelosphaeridium Beds of Furuberg Formation (lower Caradoc), northern part of the Oslo Region. The type derives from a loose boulder, but equivalent sediments and associated fauna is restricted to the Toten–Brummundalen areas in the northernmost part of the Oslo Region.

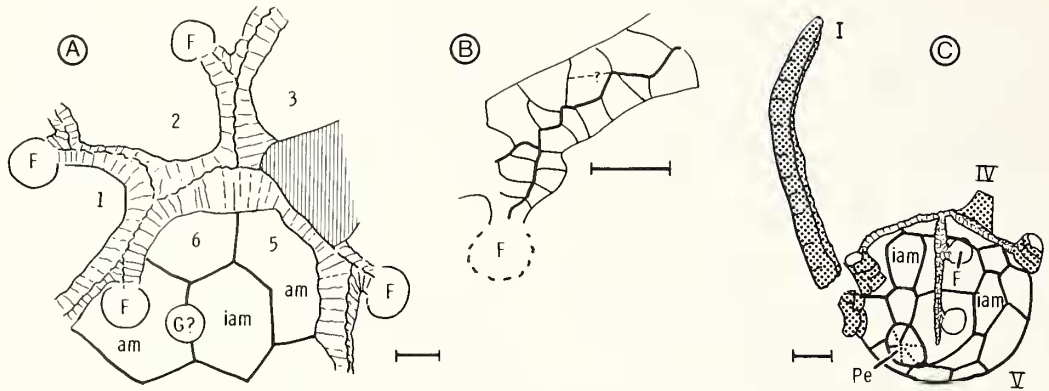
Material. In addition to the holotype, seventeen specimens (sixteen of which derive from the same boulder) are considered to belong to this species.

Description. Theca: egg-shaped, height/width ratio varies between 1.2 and 1.7.

Plates: about a hundred in adults. The plates are regular pentagonal or hexagonal. The main addition of new plates is considered to have taken place adoral to the basals (text-fig. 16; Pl. 1, fig. 8). The plate surface is usually strongly ornamented with nodes or spines, obliterating the diplopores. Plate thickness is approximately 1 mm. The sutures between contiguous plates are irregular and interlocking like those of *Celticystis* (Bockelie 1979b).

Diplopores: with or without a periporal rim; periporal floor below thecal surface. Diplopores seem to have been present on all thecal plates including the basals. The peripores are relatively small, seldom exceeding 0.40×0.25 mm.

Peristome: 1×2 mm in adults. In PMO 101.136, CO5 and CO6 may be partly fused, but in other specimens a clear suture is present. The mouth is covered by numerous ambulacral cover plates which are somewhat bigger



TEXT-FIG. 17. *Protocrinites rugatus* n. sp. A, PMO 101.130, oral area showing six circum-oral plates (1-6) and the relationship of ambulacral plates (am) to the inter-ambulacrals (iam); ambulacral cover plates continue from brachioles towards and on to the mouth as oral cover plates. B, PMO 101.133, details of ambulacrum with cover plates of variable shape. C, PMO 101.458, juvenile specimen with complete brachiole in radius I (dotted); each ambulacrum has two brachioles; no gonopore developed. G?, gonopore; F, brachiole facets; vertically ruled area not exposed; scale bars 1 mm.

than cover plates in other parts of the theca (text-fig. 17A; Pl. 1, fig. 3). The ambulacral grooves are approximately 1 mm wide and covered by large triangular plates along their sides, with smaller often irregular plates intercalated. Towards the base the ambulacral grooves become thinner (0.25 mm). The food grooves continue on to unbranched biserial brachioles (text-fig. 17A; Pl. 1, figs. 1, 5-8), the largest of which measures 15 mm. Two cover plates seem to be attached to each brachiole element (text-fig. 13; Pl. 1, fig. 7). The structure of the brachioles thus may resemble that of the eocrinoid *Gogia longidactylus* (Sprinkle 1973, text-fig. 10).

Periproct: large, round, 2.5-3.5 mm in diameter and covered by an anal pyramid of five or six triangular plates (Pl. 1, fig. 6). The periproct lies about mid-height in interradius V-I separated from the mouth by three plate series (text-figs. 16, 17).

Gonopore/hydropore: a tubercle present on the CO5:CO6 suture, or at the suture between adambulacral and interambulacral plate just below CO6, may be a hydropore.

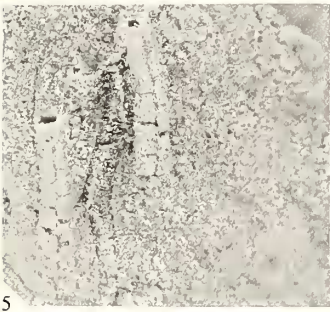
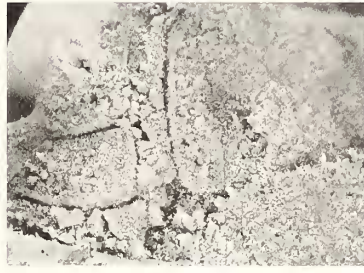
Attachment: a flexible stem was present in life, with complex nodals and internodals. The stem is similar to that of crinoids, and at least 8 mm long.

Palaeoecology. I believe that they all lived in fairly shallow clear water, on a muddy bottom with few properly sessile elements, in an area commonly covered by coarser sediments at irregular intervals.

Remarks. *P. rugatus* differs from other *Protocrinites* species in the amalgamation of its basals to form a solid socket.

EXPLANATION OF PLATE I

Figs. 1-8. *Protocrinites rugatus* n. sp. Coelosphaeridium Beds, Furuberg Formation, northern Oslo Region. 1, PMO 101.138, stereophotos of holotype, $\times 3$. 2, PMO 101.132, lateral view showing two ambulacra and stem, $\times 2$. 3, PMO 101.133, stereophotos of oral area showing plate configuration and ambulacral and oral cover plates, $\times 5$. 4, PMO 101.133, lateral view showing theca and incomplete brachioles, $\times 1$. 5, PMO 101.130, stereophotos of biserial brachioles and ambulacrum with cover plates preserved, $\times 7$. 6, PMO 101.130, stereophotos showing anal pyramid and brachioles, $\times 4$. 7, PMO 101.133, brachiole with brachiolar cover plates (two cover plates to each brachiole element), $\times 5$. 8, PMO 101.132, details of ambulacrum with cover plates. The ambulacrum stops in the third plate series from the base. This is the growth zone where new plates and extensions of the ambulacrum are added, $\times 5$.



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Superfamily SPHAERONITIDA Neumayr, 1889

Diagnosis. Stemless Diploporita with variable-shaped theca; almost all plates pierced by diplopores; peristome covered by a roof (palate) of six plates beneath which food grooves pass to the mouth; four or five ambulacra; food grooves narrow, generally short but extending over theca in some species; periproct covered by pyramid of triangular plates; circular gonopore and generally slit-like hydopore between peristome and periproct, and to the left.

Remarks. Paul's (1973, p. 18) definition of the superfamily is accepted here, but whether or not cover plates where present on the ambulacra is not known.

Family SPHAERONITIDAE Neumayr, 1889

Diagnosis. 'A family of Sphaeronitida with diplopores; peristome surrounded by six circum-oral plates with a small additional plate (CO7) between the peristome and the periproct but not in contact with the former; four or five ambulacra with one or more ambulacral facets each' (Paul 1973, pp. 18, 19).

Remarks. The pore structures of Diploporita seem to be more complex than previously considered— for instance, both haplopores and diplopores have been found in the aristocystitid *Calix sedgwicki*. Some diplopores of *Eucystis* also branch in an unusual way.

Genus *Sphaeronites* Hisinger, 1828

Synonymy. See Paul (1973, p. 19).

Type species. *Echinus pomum* Gyllenhaal 1772, by original designation, p. 242, pl. 8, figs. 1–3; from the Asaphus Limestone (Arenig), Kinnekulle, Västergötland, Sweden (Regnéll 1945, pp. 162, 163).

Diagnosis. A genus of Sphaeronitidae with globular to pyriform or fusiform theca composed of approximately forty to two hundred plates which are irregularly arranged except in the oral area; peristome and periproct very close together on smooth oral prominence; five ambulacra with one to three facets each; all thecal plates uniformly covered with diplopores (except in attachment area); attachment direct.

Remarks. The diagnosis agrees with that of Paul (1973, p. 19), except that the number of brachiole facets in an ambulacrum may reach three.

Subgenus *Sphaeronites* (*Peritaphros*) Paul, 1973*Sphaeronites* (*Peritaphros*) *pauciscleritatus* Paul and Bockelie, 1983

Plate 2, figs. 2–4; text-fig. 18A

Synonymy. See Paul and Bockelie (1983, p. 723).

Diagnosis: 'A species of *Peritaphros* with large globular theca reaching 40–50 mm in diameter in adult specimens; thecal plates limited (fifty to sixty); diplopores polygonal (0.4 × 0.4 to 0.4 × 0.6 mm in adult specimens), average pore density 7.40 per mm²' (Paul and Bockelie 1983, p. 724).

Types. Holotype, PMO 79687 (Pl. 2, figs. 2, 3); paratypes, PMO 6183, 90042, 90043, 90289, 90293, 90297, 90347, 90349, 90350, 90351 (Paul and Bockelie 1983, p. 724).

Horizon and locality. Middle part of Lower Chasmops Limestone (= Stage 4bβ), middle Caradoc, Oslo-Asker District of the Oslo Region, Norway.

Remarks. Morphology and palaeoecology is described by Paul and Bockelie (1983, p. 726).

Genus *Haplosphaeronis* Jaekel, 1926

Synonymy. *Sphaeronis* Angelin, 1878 (pars); *Sphaeronis* auctorum; *Pomocystis* Haeckel, 1896; *Pomosphaera* Haeckel, 1896.

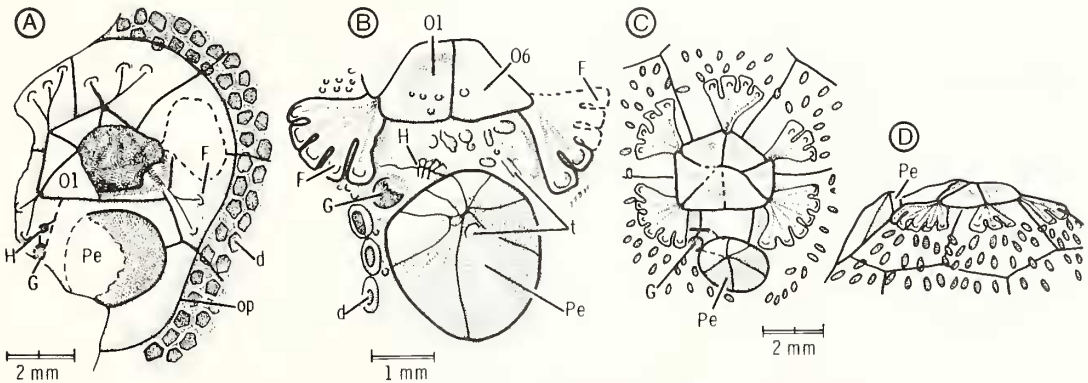
Type species. *Haplosphaeronis kiaeri* Jaekel, by monotypy, in Kiær, 1926, p. 20; from the Gagnum Shale Formation (= Sphaeronid Shale of Kiær 1926), lower Ashgill, Hadeland, Oslo Region, Norway.

Diagnosis. A genus of Sphaeronitidae with fourteen thecal plates arranged in two circlets of seven each; oval or dumb-bell shaped diplopores mostly arranged with their long axis in an ad-aboral direction; five ambulacra each with from one to ten food grooves in a fan-like arrangement at corners of peristome, confined to circum-oral plates.

Remarks. This diagnosis differs only slightly from that of Paul (1973, p. 27). Specimens containing only one groove per ambulacrum exist, especially in young specimens of at least two species. Bockelie (1978a) showed the number of food grooves per ambulacrum to increase with growth. The taxonomic value of the number of such grooves is dubious. However, stratigraphically younger species do have more grooves per ambulacrum than older species with the same thecal diameter. The type specimen of the genus is lost or mislaid; it has not been in the type collection for at least twenty-five years.

Description. The thecae of *Haplosphaeronis* are variable in shape, both between and within species. Mostly they are spherical or pyriform, but almost flat disc-shaped specimens occur. Many Norwegian specimens are shaped like an inverted pear or are mitre-shaped. British and Swedish species have a pentalobate outline in some populations. No stem is present. Most Norwegian specimens of both species are small, seldom exceeding 15 mm in diameter. In Sweden, however, individuals reaching 45 mm in height and 30 mm in diameter occur locally.

Plates: there are two circlets each with seven plates. The lower circlet has more or less equal-sized plates, while the upper circlet has five large plates bearing the ambulacra and two smaller plates (CO6 and CO7) inserted between the peristome and the periproct (text-fig. 11c). Jaekel's (1926, p. 19) original description of the genus appears to be correct, as discussed by Paul (1973, p. 28). Individual plates are thick (approximately 1 mm) and pierced by numerous diplopores. Little is known of the plate meshwork. However, silicified specimens often show the inner portion of the plates to be silicified more easily than the outer portion. Pyritization also occurs by filling the mesh of the inner portion of the plate more frequently than the outer part. By analogy with *Archaeocystis*, as described by Paul (1971, p. 11), and with *Parasphaeronites* n. gen., one may assume the



TEXT-FIG. 18. A, *Sphaeronites* (*Peritaphros*) *pauciscleritatus* Paul and Bockelie, PMO 79687 (see Pl. 2, figs. 2, 3); oro-anal area showing four oral cover plates (O1, etc.), hydropore (H), gonopore (G), and periproct (Pe) on the oral platform (op) which is devoid of diplopores (d). B, *Haplosphaeronis kiaeri* Jaekel, PMO 89972 from 5.5 to 6.0 m level, Gagnum Shale, Tønnerud, Hadeland; oro-anal area showing oral cover plates (O1, O6), major thecal openings, and characteristic tubercular ornament (t). C, D, *Haplosphaeronis bratterudensis* n. sp., PMO 89201 from Lower Chasmops Limestone, Bratterud, Ringerike, holotype; C, from above and D, in lateral view (note the radiate pattern of diplopores).

presence of an outer fine mesh and an inner coarse mesh. Weathered specimens of *H. cf. kiaeri* from 16 to 17 m below the top of the Upper Chasmops Limestone at Raudskjær, Asker, show the crystallographic orientation of palatals covering the mouth (text-fig. 20H). One weathered specimen (PMO 90965) shows fine lineations, representing cleavage, within the calcite plates. The direction seen on one plate always differs from those of the adjoining plates. The angle of dip cannot always be ascertained, but the direction of dip changes from one plate to the next, e.g. O1, O3, and O5 dip away from the mouth, whereas O2, O4, and O6 dip towards the mouth. A similar pattern has also been observed in other specimens, and may be typical for *Haplosphaeronis* species in general. All thecal plates have numerous rather specialized diplopores. Small knobs or tubercular ornament may be present between the diplopores. Occasionally these are either new pores in the process of formation, or pores that have been reduced.

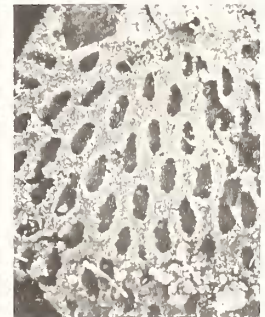
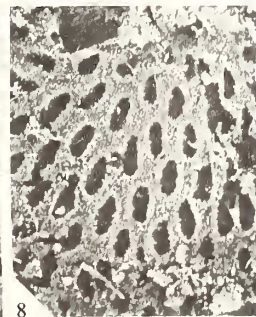
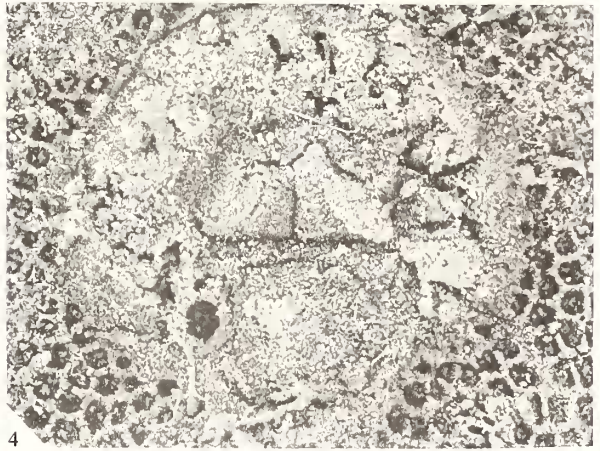
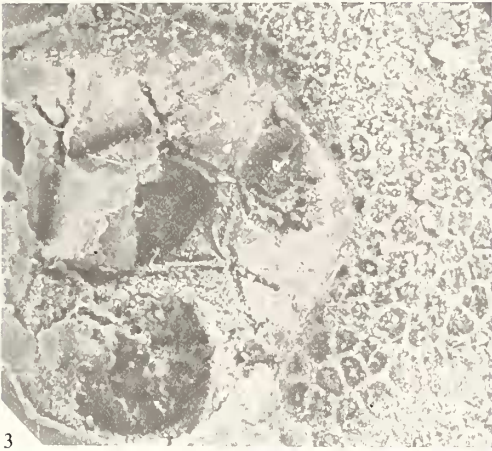
Thecal openings: the peristome is large and covered by six palatals (Paul 1971), two of which may be almost fused (O1 and O6). The palatals are arranged in the usual manner for sphaeronitids (text-fig. 11C). The periproct is oval or pyriform with a covering pyramid of five to seven anals. The apex of the anal pyramid is frequently directed towards the oral region (text-fig. 18D). Laths are developed on the inside of the lower edge of the periproct, as also seen in *Tetreucystis* n. gen., and this suggests that three or four of the lower plates of the anal pyramid were able to open outwards, whereas the adorally located pyramid plates were not flexible (text-fig. 26B, C; Pl. 2, fig. 6). This arrangement would have permitted faecal matter to fall down over the theca into the zone of maximum current velocity around the theca and thus be transported away from the animal. The faecal matter was probably in the form of small pellets. Between the peristome and the periproct, and to the left, is a small usually circular gonopore and a slit-like hydropore (text-fig. 18B). The hydropore is always located on top of a slightly elevated ridge, reducing the possibility that sediment particles would have entered the slit. The gonopore may have been covered by a pyramid of small triangular plates, but this has never been observed. Such plates are only known in fistuliporite Rhombifera.

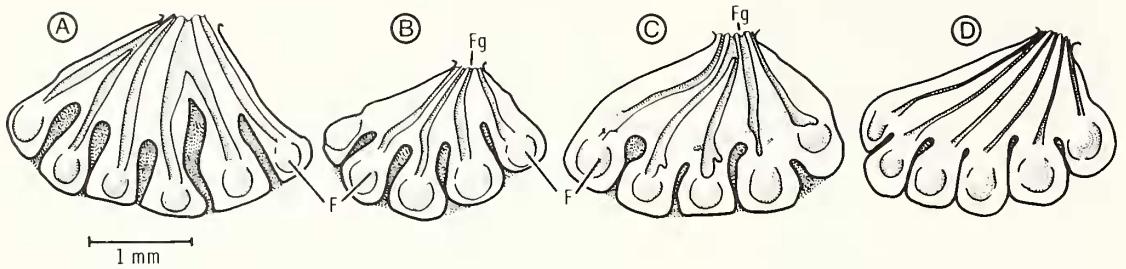
Diplopores of *Haplosphaeronis* are mostly elongated and typical of the genus. They are numerous and spread over the thecal surface, usually aligned in an ad-aboral direction. However, some of the pores near the plate edges (probably the last ones formed) are set perpendicular to this direction. In stratigraphically older species the perpendicular arrangement of diplopores is absent (Pl. 2, figs. 7, 8). In the circum-oral plates the diplopores are arranged in a fan-like manner (Pl. 3, fig. 3) with diplopores in rows. The number of rows gives some indication as to how many growth stages the cystoid has gone through (e.g. a specimen with five rows is probably older than a specimen with only three rows). As many as twelve rows have been observed in some specimens of *H. proiciens* Regnéll. The length and width of individual peripores in the different rows may vary. The diplopores at plate sutures are often smaller than other pores of the theca. It seems that new diplopores were added at plate sutures throughout the growth of the theca, and reached maximum size fairly rapidly.

Ambulacral system: the peristome is always pentagonal and may have five raised ambulacral platforms at the corners. One to ten food grooves radiate in a fan-like pattern on each ambulacral platform and terminate in small (usually 0.5 mm in diameter) ambulacral facets at the outer edge (text-fig. 19). The brachioles were biserial, as indicated by the small ridge between the pair of muscle-scars on each facet. The ambulacral furrow leading to the first formed facet is always perpendicular to the adjoining oral edge, whereas later ones are not. Between adjacent ambulacral facets and their ambulacral structures, ridges are developed to separate them. These ridges are of different types and details of their structure may be of some taxonomic importance. Two main shapes of facet

EXPLANATION OF PLATE 2

- Fig. 1. *Sphaeronites (Peritaphros) globuhus* (Angelin). Dalby Limestone, Böda Harbour, Öland, Sweden. RM Ec 4360, stereophoto of holotype showing oral-anal region, approximately $\times 10$.
 Figs. 2-4. *Sphaeronites (Peritaphros) pauciscleritatus* Paul and Bockelie. Lower Chasmops Limestone, Fyrsteilen, Oslo-Asker. 2, 3, PMO 79687, cast of holotype showing 2, diplopores and 3, oral view of oral area, $\times 6$. 4, PMO 90042, cast of oral area in oral view, Hareholmen at Ostoya, Bærum, $\times 6$.
 Figs. 5-8. *Haplosphaeronis bratterudensis* n. sp. Lower Chasmops Shale, Bratterud, Ringerike. 5, PMO 89201, cast of holotype, stereophoto of oro-anal area (specimen whitened with ammonium chloride sublimate), $\times 4$. 6, PMO 89202, stereophoto of cast showing anal region with shelf for attachment of anal plates in aboral side, $\times 7$. 7, PMO 89209, stereophoto of cast showing diplopores in circum-oral plates, $\times 6$. 8, PMO 89213, stereophoto of cast showing diplopores in basal plates, $\times 6$.





TEXT-FIG. 19. Brachiole facets of *Haplosphaeronis* species. The stratigraphically oldest species to the left, the youngest to the right. A, *H. bratterudensis* n. sp., PMO 89201, holotype. B, *H. cf. kiaeri* Jaekel, PMO 102.757, from Solvang Formation, Gagnum Farm, Hadeland. C, *H. kiaeri* Jaekel, PMO 101.939, from Gagnum Limestone (27–28 m level), Tønnerud, Hadeland. D, *H. multifida* Paul, SM A 74796, original of Paul (1973, pl. 2, fig. 3). The oldest species has angular facets with deep incisions while later species have more rounded brachiole facets with small incisions, if any.

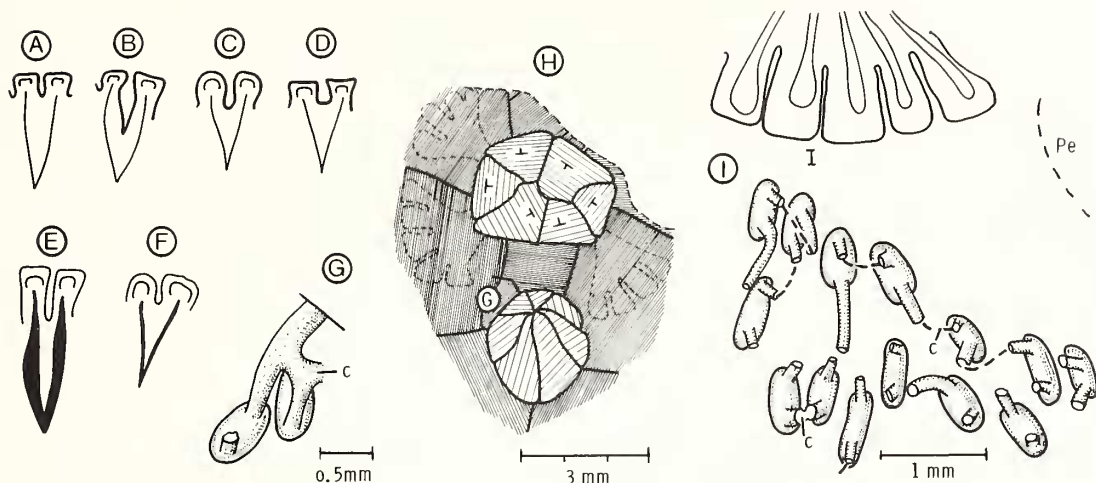
have been observed: ones with rounded edges and ones with square or angular edges (text-fig. 20c, d). The incisions between adjacent facets may be of two types: either deep and broad incisions, leaving fairly large spaces between individual facets, or small and narrow incisions, only just separating the outer edges of individual facets (text-fig. 20A, B). The deep incisions are found mostly amongst the earliest species and the smaller incisions amongst later ones. Both types can occur together in the same individual.

Nerve system: both a basal and an oral nerve ring occur in *Haplosphaeronis*. Paul (1973) also suggested the presence of an oral nerve ring, and nerve canals entering individual brachioles at their facets. Details of this are not known.

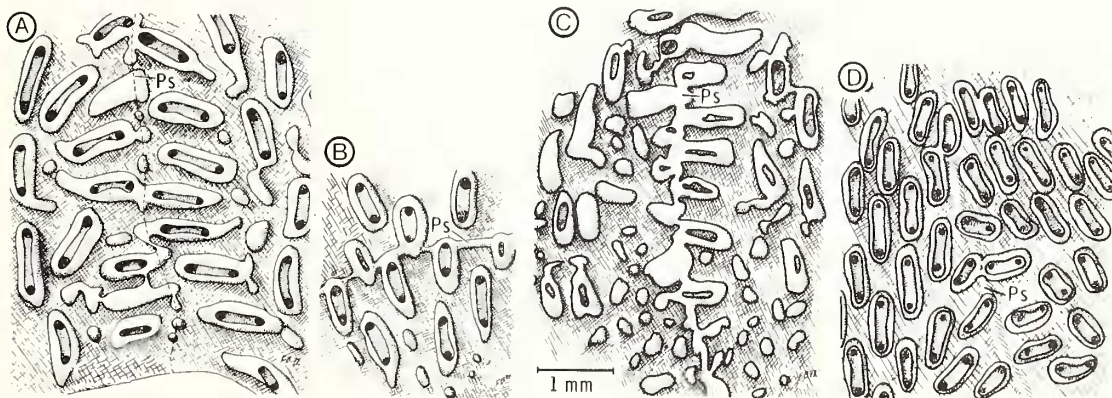
Attachment: all *Haplosphaeronis* species were attached directly by their base. The attachment area is usually concave and adjusted to the shape of objects to which thecae were attached. Specimens of *Haplosphaeronis* have been found attached to other *Haplosphaeronis* individuals, to stick bryozoa, brachiopods, cephalopods, trilobites, and crinoid ossicles. Many specimens show no imprints of the objects to which they were attached, and may thus either have been attached to soft-bodied animals, such as ascideans, or to algae.

Ontogeny and phylogeny. The shapes and sizes of individuals of *Haplosphaeronis* (and other cystoids) depend on the environmental conditions, such as substrate, nutrition, etc. Details of growth pattern can only be obtained through studies of large samples. Individuals from populations at different stratigraphical levels may vary considerably.

Ontogeny: in some populations it is possible to study parts of the ontogeny, but usually the youngest individuals (less than 5 mm) are extremely rare. The major thecal openings (mouth, anus, gonopore, and hydropore) increased in size isometrically during ontogeny. The number of thecal plates remained constant, and thecal size only increased by accretionary growth along the sides of individual plates. The attachment area increased with growth, but no relationship exists between the size of the attachment area and the size of the animal. The most striking ontogenetic change was in the addition of new ambulacral facets. Very young individuals all appear to have had one facet only in each of the five ambulacra (see Bockelie 1978a). New facets were added continuously during growth but, at a stage which might be interpreted as adult, a sudden rapid increase occurred. Whereas the number of brachioles in Norwegian adult *Haplosphaeronis* is relatively large, the total number of Swedish specimens of *H. oblonga* of the same diameter is lower. One explanation is that the brachioles of Swedish species were longer; alternatively, the uptake of food was greater in Swedish than in Norwegian populations. The addition of new diplopores during growth is not clearly understood, but possibly new pores were formed by resorption of the skeletal mesh. Pores were added throughout thecal growth. Pores close to the plate sutures are usually smaller than those towards the plate centre, which may indicate that they grew until a certain size was reached. It seems that the initial growth was more rapid than the later growth. The growth rates of thecae of *Haplosphaeronis* species may be different (text-fig. 24), resulting in different shapes.



TEXT-FIG. 20. Morphological features of *Haplosphaeronis*. A-F, types of brachiole facets and food grooves showing A, small incisions between facets; B, deep incisions between facets; C, rounded fringes of facets; D, angular fringes of facets; E, wide or expanded food grooves; and F, narrow food grooves. G, *H. cf. kiaeri* Jaekel, PMO 89933, from Upper Chasmops Shale, Solheim-Rud, Ringerike; connections of peripores within thecal wall showing two diplopores connected and possible connection to a third diplopoire (c). H, *H. cf. kiaeri* Jaekel, PMO 90965, from Upper Chasmops Limestone, 16-17 m below Tretaspis Shale, Raudskjær, Asker; orientation of cleavage planes (?) and direction of dip in weathered specimen (note that direction of dip alternates regularly from one oral plate to the next). I, *H. cf. kiaeri* Jaekel, PMO 105.893, middle part of Upper Chasmops Limestone, Nesbrukryset, Asker; inside, showing connections of pyritized diploporic canals (c).



TEXT-FIG. 21. Diplopores of *Haplosphaeronis*. A-C, *H. kiaeri* Jaekel from Gagnum Shale (5.5-6.0 m level), Tønnerud, Hadeland. D, *H. proiciens* Regnéll from near Fauquez, Belgium. *H. kiaeri* has irregular diplopores and these are often covered with a calcified periporal roof, whereas this is not so with *H. proiciens*. A, PMO 89924, basal plate. B, PMO 89970, showing boundary between circum-oral plate and basal plate. C, PMO 89920, basal plate with most diplopores covered. D, IRScNB 16c, basal plate showing sutural area. Ps, plate suture.

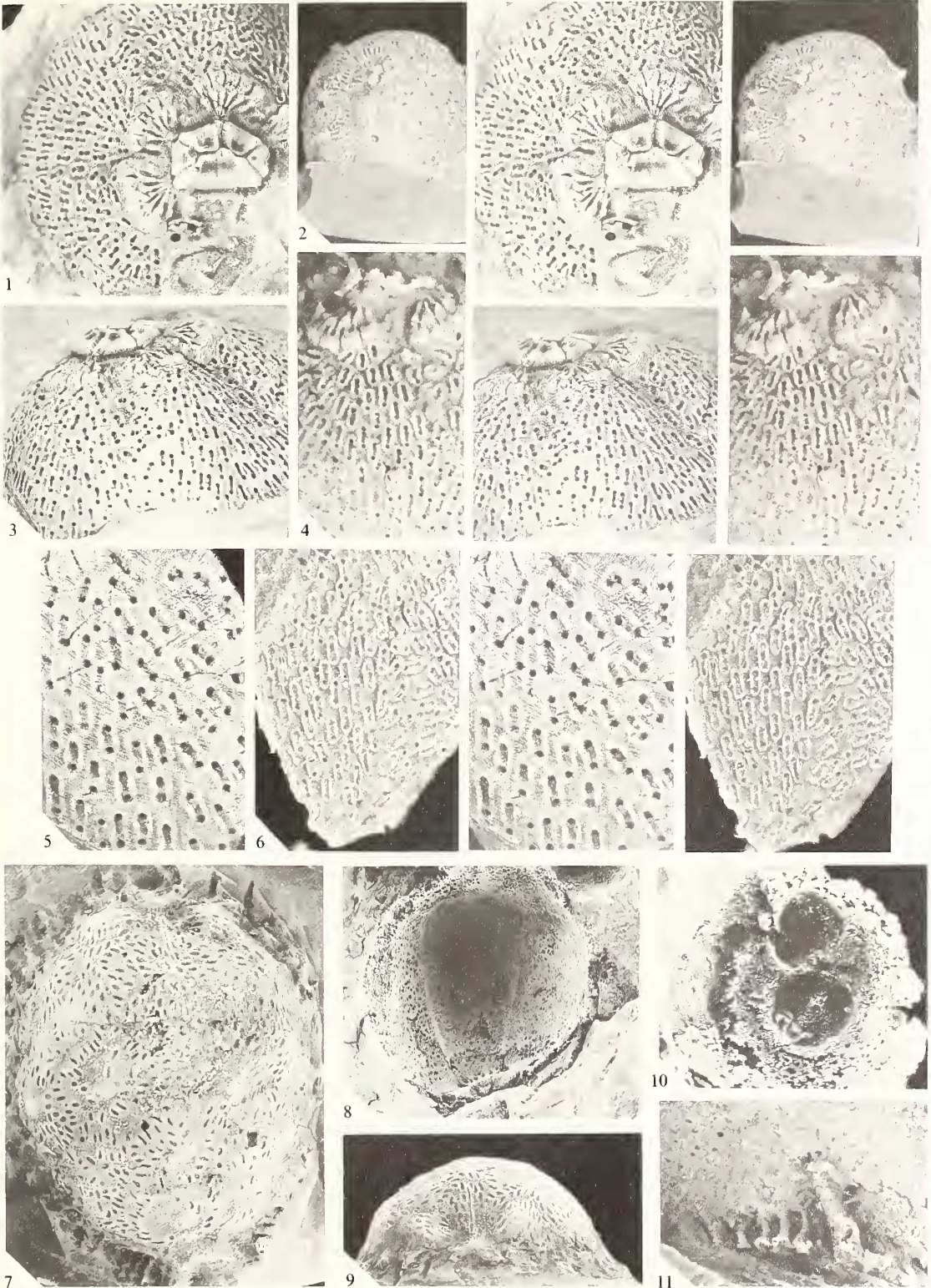
Phylogeny: Norwegian *Haplosphaeronis* ranged from the Caradoc to the lower part of the Ashgill and occurred in several different environments. Species morphology is to some extent a reflection of the environmental conditions under which they lived. When phyletic trends are sought, it should be kept in mind that we do not always see the same type of environment. The pattern of phyletic changes is often very complicated when several environments of the same age are preserved, as is the case with *Haplosphaeronis*.

The number of brachiole facets per ambulacrum is generally larger in Ashgill than in Caradoc populations of individuals with the same thecal diameter. In Norway this is certainly the case. In Sweden this cannot be conclusively stated. In Britain *Haplosphaeronis* occurs in the Ashgill only where the species has numerous brachioles. The shape of brachiole facets changes from the lower Caradoc *H. bratterudensis* to the Ashgill *H. kiaeri*. *H. bratterudensis* always has square facets separated by large spaces, often with deep incisions (text-fig. 19). In *H. kiaeri* the facets are rounded or tongue-shaped and not separated by spaces (text-fig. 19C, D). During the later Caradoc several morphs combined the two types of brachiole facets (text-fig. 19B), clearly showing the direction of evolution. The British *H. multifida* has facets of the same type as the Ashgill species in Norway.

The most striking evolution is seen in the pore structures, which may be good stratigraphical indicators (see above). The oldest species in Norway, *H. bratterudensis*, has faintly developed rims around the diplopores or no rims at all; the peripore floor is sunk well below the thecal surface; the peripore is ovate with a length to width ratio of 3.6. In the late middle Ordovician and the upper Ordovician the diplopore floor migrated outwards to a position above the thecal surface. In the latest populations of *H. kiaeri* from the Oslo Region the aporal portion of the peripore wall developed spines (Pl. 5, fig. 3). Such spines have also been found in the British Ashgill species, but not in the Belgian Ashgill species which is otherwise very similar. The shift of the peripore floor from a deep to an outer position, and the outgrowth of the peripore wall to form spines accompanied by a narrowing of the diplopores in relation to pore length (length to width ratio is 4.5), is clearly part of a continuous evolution (text-fig. 25). Thus the length to width ratio of the diplopores increased from 3.6 to 4.5 during the Ordovician principally by a reduction of pore width. There was also some reduction of pore length (text-fig. 25). This change is accompanied by an increase in number of diplopores in some (but not all) populations of *H. kiaeri*. Narrow diplopores have been seen in the British and Belgian species (Pl. 3, fig. 6). The changes in diplopore shape during the Ordovician may be related to

EXPLANATION OF PLATE 3

- Figs. 1–5. *Haplosphaeronis* cf. *kiaeri* Jaekel. 1, 3, 5, Upper Chasmops Limestone, Raudskjær (8 m below top), Asker; PMO 69421, stereophotos of 1, oral area (note slightly lobate shape of theca, and complex hydropore with slit and circular opening), $\times 4$; 3, circum-oral plates showing diplopores with thickenings and spines on peripore wall, $\times 4$; 5, circum-oral plates and lateral plates showing details of diplopores (note development of spines on peripore walls, irregular diplopores at the plate suture to the right, and the thickness of the walls), $\times 7$. 2, 4, Solvang Formation, Gagnum Farm, Hadeland; PMO 102.759, stereophotos of silicone rubber cast showing 2, oral region, $\times 4$; 4, circum-oral plates with spines on peripore wall, $\times 6$.
- Figs. 6, 11. *Haplosphaeronis proiciens* Regnéll. Ashgill, near Fauquez, Belgium. 6, IRScNB 16c, stereophotos of plates showing development of spines on peripore wall (silicone rubber cast; note the very thin walls in comparison with fig. 5, and diplopores in horizontal position at the plate suture), $\times 6$. 11, IRScNB 199–1, basal portion of theca showing depressions which possibly housed extensions of basal nerve ring (silicone rubber cast), $\times 5$.
- Figs. 7, 9. *Archaeogocystis* cf. *granulata* Paul. Sørbakken Limestone, Frognoya, Ringerike. PMO 97106 in 7, lateral view (note radial arrangement of elongate diplopores and granulated surface) and 9, showing oral area (outermost portion of two brachiole facets and a plate suture), $\times 2.5$.
- Figs. 8, 10. *Haplosphaeronis kiaeri* Jaekel. Gagnum Limestone, Tønnerud, Hadeland. 8, PMO 79921 from 14 m level, inside of theca showing plate sutures and depressions along inside of base, possibly a location for basal nerve ring with thickenings, $\times 2$. 10, PMO 91008 from 27–28 m level, showing inside of oral (smallest depression) and anal (largest depression) areas, with a furrow which previously housed the gonoduct leading from the right side towards and between the mouth and anus before entering the body cavity, $\times 3$.



BOCKELIE, *Haplosphaeronis* and *Archaeogocystis*

increased efficiency of respiration. Evolutionary changes in respiratory structures have also been seen in other cystoids.

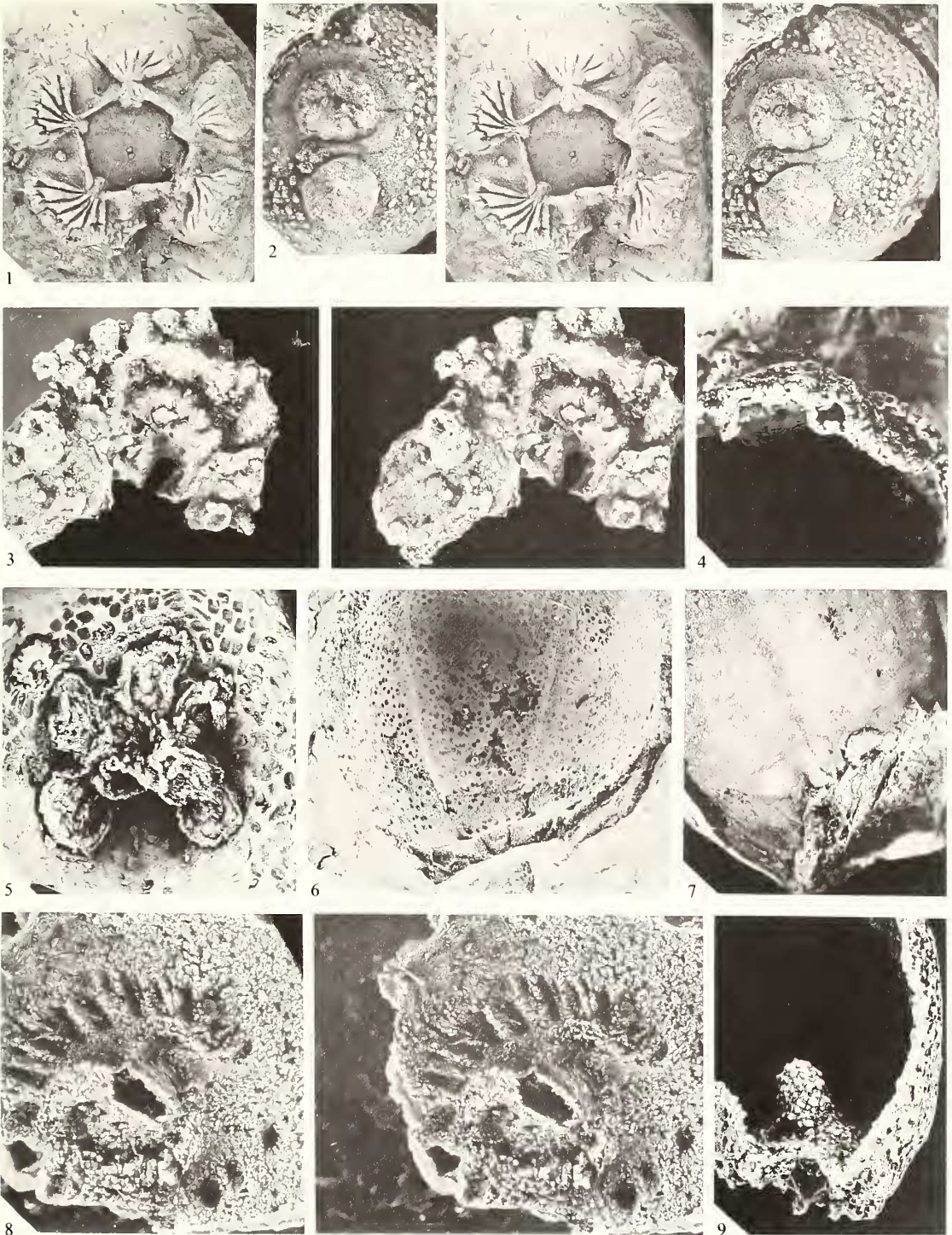
Upper Ordovician *Haplosphaeronis* species from Norway and Britain commonly have calcite-covered diplopores either in their basal portion, on their circum-oral plates, or occasionally all over the theca. Belgian and Swedish upper Ordovician species have not been found with covered pores; neither have they been found in the lower and middle Caradoc populations of *H. bratterudensis* and *H. kiaeri*. Whether covered pores are a response to local environmental conditions, some kind of disease, or a phyletic trend towards some kind of physical protection is not clear. Covered diplopores are relatively common amongst the *Diploporita*.

Palaeoecology. *Haplosphaeronis* seems to have occupied a wide range of ecological niches, and is found in rocks representing environments ranging from shallow, turbulent water to depths just below the wave base. They are distributed mostly in areas of regular sedimentation rates and dominate certain environments in the western part of the Oslo Region. In Sweden *Haplosphaeronis* species are common on the flanks of most carbonate mounds ('reefs') of middle and upper Ordovician age (Kullberg Limestone and Boda Limestone). British species were adapted to environments with more clastic sediments and are found in silts or shales with small amounts of carbonate (Paul 1973, p. 29). The shape of the attachment area is probably related to environmental position. The shallow water Swedish species were often attached to a firm substrate or large crinoid ossicles; the Norwegian species may have been attached mostly to small objects and needed to grow rapidly upwards to compensate for rapid sedimentation, giving *H. kiaeri* a characteristic mitre shape. The Swedish species in contrast, living in areas of low sedimentation rates, have a flat base.

Remarks. The holotype of the Swedish *H. oblonga* (RM Ec96) derives from the upper Ordovician Boda Limestone, and not from the middle Ordovician as previously stated by various authors. Regnéll (1945, p. 171) made all the species of *Haplosphaeronis* erected by Angelin synonyms of *H. oblonga*. *H. oblonga* thus comprises all Swedish *Haplosphaeronis* species and ranges from the lower Caradoc (Dalby Limestone) to the middle-upper Ashgill (parts of the Boda Limestone). It is rare to find species with such a long range. However, Angelin's species are all strongly corroded and his distinctions were mostly based upon differences in size. In view of the evolutionary changes found amongst Norwegian species, it seems justified to expect similar changes to have taken place in Swedish populations. Thecal shape shows great variation and may be more related to ecological factors than to anything else. The number of facets was ontogenetically controlled, at least in part (Bockelie 1978a). The shape and distribution of the diplopores currently seem to have most taxonomic value.

EXPLANATION OF PLATE 4

Figs. 1-9. *Haplosphaeronis kiaeri* Jaekel. Tønnerud, Hadeland. 1, PMO 101.939, stereophoto of oral area showing peristome with ambulacral platform entering mouth, $\times 5$. 2, PMO 89996, stereophoto of steinkern showing peristome, periproct, and traces of gonoduct (note lack of diplopores in oral and anal area; gonoduct goes down through the plate, is embedded horizontally in the plate between peristome and periproct, and bends towards radius IV before entering the thecal interior), $\times 5$. 3, PMO 101.954, stereophoto of silicified specimen in oral view (just below peristome looking down oesophagus) showing one oral lobe and parts of two more; upper part of gonoduct at left (cf. text-fig. 23A), $\times 6$. 4, PMO 90976, sagittal view of silicified specimen showing cavities within circum-oral plates below ambulacral facet (cf. text-fig. 23B), $\times 4$. 5, PMO 91007, inside view showing circum-oral lobes and parts of oesophagus(?), $\times 4$. 6, PMO 79921, basal portion of pyritized specimen showing large primary depressions at plate sutures around basal ring, and several minor depressions, $\times 3$. 7, PMO 79885, steinkern showing depressions (as lobes), $\times 4$. 8, PMO 101.953, stereophoto of silicified basal portion of theca possessing hollow internal spine, surrounded by outer wall and several local depressions (see also text-fig. 22A, D), $\times 6$. 9, PMO 91004, coarsely silicified specimen showing internal spine (cf. text-fig. 22B, C), $\times 4$. 1, 3-5, 8, 9, 27-28 m level and 7, 18-20 m below Solvang Formation in Gagnum Limestone; 2, 5.5-6.0 m level and 6, 14 m level in Gagnum Shale.



BOCKELIE, *Haplosphaeromys*

Sphaeronites shihtienensis Reed, of which no specimens were available for study, was referred with some hesitation to *Haplosphaeronis* by Regnéll (1945, pp. 170, 171). This species, however, differs from both *Sphaeronites* and *Haplosphaeronis* and in my opinion does not belong to the Sphaeronitidae, but to the Aristocystitidae.

Regional distribution and stratigraphical range. Oslo Region (middle–upper Ordovician), Sweden (middle–upper Ordovician; Regnéll 1945, p. 171), southern Estonia (middle Ordovician; Männil 1966, pp. 41, 43, 45), Ingermanland (middle Ordovician; Hecker 1964, pl. 4), Wales (upper Ordovician; Paul 1973, p. 3), Belgium (upper Ordovician; Regnéll 1951, p. 31), and Burma (Ordovician; Reed 1917, p. 12).

Haplosphaeronis kiaeri Jaekel, 1926

Plate 3, figs. 8, 10; Plate 4, figs. 1–9; Plate 5, figs. 1–4; text-figs. 18B, 19C, 21A–C, 22, 23

1926 *Haplosphaeronis kiaeri* Jaekel, p. 20, pl. 1, figs. 1–7.

1926 *Haplosphaeronis kiaeri* Jaekel; Kiær, p. 8.

1945 *Haplosphaeronis kiaeri* Jaekel; Regnéll, pp. 171–174.

1945 *Haplosphaeronis kiaeri* Jaekel; Størmer, p. 381.

1953 *Haplosphaeronis kiaeri* Jaekel; Størmer, pp. 68, 87, 94.

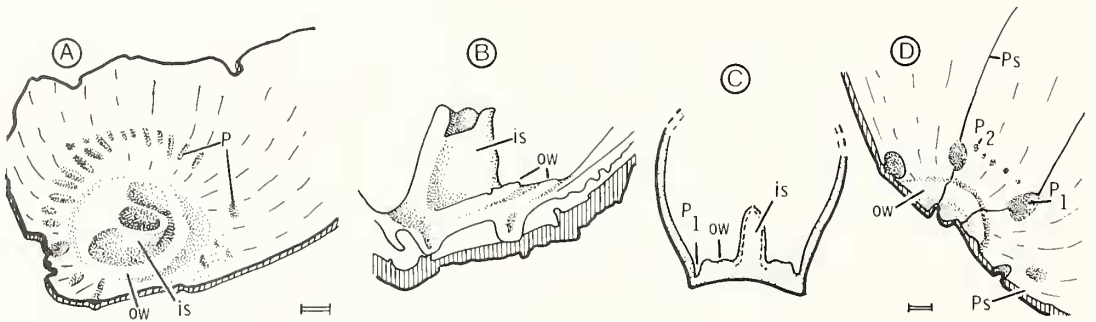
Diagnosis. A species of *Haplosphaeronis* with peripores elevated above the thecal surface or level with it, their periporal walls often developed as high ridges in the adoral portion. Diplopores often coalescent, usually irregular or oval, occasionally dumb-bell shaped, most numerous in circum-oral plates, but strongly reduced in size and number in the basals where they are covered by a calcified diplopore roof. Tubercles may be present over most of the thecal surface and are most numerous in the basal circum-oral areas.

Holotype. Unnumbered specimen in the PMO collections; pl. 1, figs. 1, 2 of Jaekel (1926). It has not been in the PMO collections for at least twenty-five years and is probably lost. Topotype material exists in the PMO collections.

Type horizon and locality. Gagnum Shale Formation (= Sphaeronid Shale), lower Ashgill; Tønnerudodden, Hadeland, Oslo Region, Norway.

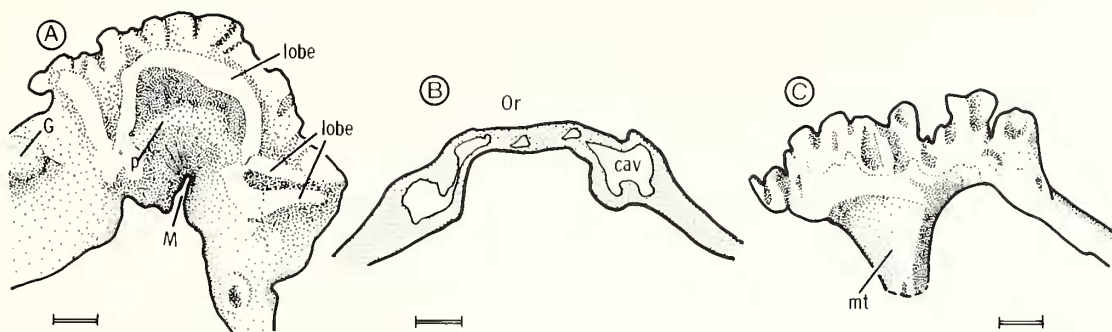
Material. Several hundred specimens.

Description. Theca: taller than broad, seldom exceeding 15 mm in height and 10 mm in diameter. The base is variable in shape and size.



TEXT-FIG. 22. Internal features of *Haplosphaeronis kiaeri* Jaekel. A, B, PMO 101.953, from Gagnum Limestone (27–28 m level), Tønnerud, Hadeland; silicified specimen showing internal spine (is), a basal wall structure (ow), and basal pits (P) in A, oblique view and B, lateral view. C, reconstruction in sagittal view showing hollow internal spine (is), wall structure (ow), and primary basal pits (P_1). D, PMO 79921, Gagnum Limestone (14 m level), Tønnerud, Hadeland; oblique view of basal portion of pyritized theca showing basal wall (ow), plate sutures (Ps), and primary (P_1) and secondary (P_2) pits (note that primary pits are located at the plate sutures).

Scale bar, 1 mm.



TEXT-FIG. 23. Internal features (oral region) of *Haplosphaeronis kiaeri* Jaekel from Gagnum Limestone (27–28 m level), Tønnerud, Hadeland; silicified specimens. A, PMO 101.954, oblique view from oral area showing lobate circum-oral ring structure with steep sides down to the platform (p), and the slope down into the mouth tract (G, gonopore); this silicified portion is just below the calcite skeleton of the oral area. B, PMO 90976, lateral view showing silicified theca with a circum-oral cavity within the skeleton, and the oral plates (or). C, PMO 101.954, lateral view of A showing irregular upper portion of the mouth tract (mt). Scale bar, 1 mm.

Plates: all except CO6 and CO7 are pierced by numerous diplopores. An ornament frequently occurs between the diplopores of the basal plates and is characteristic of some populations. This surface ornament is usually reminiscent of calcified diplopores.

Diplopores: small; many coalesce or have irregular extensions (text-fig. 21). The peripores are oval, averaging 0.49×0.11 mm (text-fig. 25). The periporal floor is usually elevated above the thecal surface. Various populations have the aporal portions of the periporal rims developed with thickenings of the wall (Pl. 5, fig. 3). No specimens have been found within the type stratum with more than twenty facets. The small size of the animals may indicate a stunted population. There are pronounced thickenings of the sides of the food grooves, as seen also in the British species *H. multifida* Paul. Facets usually have a rounded outline but more irregular shapes occur; they are 0.28–0.32 mm in diameter and have a slightly raised circular central process (text-fig. 19c).

Periproct: size related to animal size; 4.2×3.6 mm in PMO 89972. Plates of the anal pyramid occasionally bear small tubercles near the summit.

Gonopore: small circular pore, 1.3 mm in diameter in PMO 89972, almost in contact with the first facet in radius I.

Hydropore: a slit of variable length. In PMO 89972 it is zigzag shaped and very irregular.

Attachment: direct, by an aboral attachment area, usually one-third to one-half the ambital diameter.

Remarks. Jaekel (1926) distinguished two subspecies by size, *H. k. kiaeri* and *H. k. norvegica* (the latter not figured). *H. k. kiaeri* came from the Gagnum Shale Formation (= Sphaeronid Shale) and *H. k. norvegica* from the overlying Gagnum Limestone Formation (= Sphaeronid Limestone). The morphology of the pore system shows a rather complex relationship between *H. bratterudensis* n. sp. and *H. kiaeri*. It is difficult to decide at present whether or not a subspecific determination can be made, due to the observed continuous morphological series. Jaekel's concept of *H. k. norvegica* is not clear nor did he state from which part of the limestone his material was derived. Differences in size of *Haplosphaeronis* in these populations are due to various ecological features. They may reflect differences in sedimentation rates which killed off certain populations at different growth stages. Other populations could have been stunted by low rates of nutrition.

H. kiaeri differs from *H. bratterudensis* n. sp. in that the latter has wider peripores and a peripore floor sunk below the thecal surface. *H. kiaeri* differs from the Belgian *H. proiciens* by the latter's lack of ornament and irregularities in the peripore wall. *H. kiaeri* differs from *H. multifida* by the lack of elevation of the oral area (in this respect *H. multifida* resembles *H. proiciens*). *H. multifida* has larger diplopores than *H. kiaeri* (length 0.64 versus 0.49 mm; width 0.21 versus 0.11 mm). *H. kiaeri* differs from *H. oblonga* in general shape, the latter always having a broad flat base and relatively few brachioles in relation to thecal size. However, the Swedish species also lacks ornament on the basal

plates as well as the irregularities of the periproctal rims seen in *H. kiaeri*. *H. oblonga* is difficult to define; specimens from 10 to 12 m below the main bentonite band of the Dalby Limestone up to the Boda Limestone itself have all been referred to *H. oblonga*, giving that species a vertical range which includes most of the middle and all the upper Ordovician. This is most unlikely and several species may be involved. Differences in size of specimens occurring in off-reef and reef facies have also been observed in Dalecarlica, the reef forms being larger. *H. kiaeri* resembles the British *H. sparsipora* more than any other species, but the latter has very wide peripores (0.26 versus 0.11 mm). The peripore length of *H. sparsipora* is 0.54 mm and falls just within the range of variation in *H. kiaeri*.

Numerous populations of *Haplosphaeronis* occur in the middle Ordovician of the Oslo Region, mostly in the upper Caradoc of Oslo-Asker (Upper Chasmops Limestone), Skien-Langesund area (Encrinite Limestone), Ringerike (Solvang Formation), and Hadeland (Solvang Formation). These all differ from typical *H. kiaeri* in being transitional between the early Caradoc species *H. bratterudensis* and the Ashgill species *H. kiaeri* (Pl. 3, fig. 3). However, this transition is so complex that at present I prefer to place these upper Caradoc populations in *H. cf. kiaeri* since they show closer affinities to *H. kiaeri* than to *H. bratterudensis*. They usually have peripore rims, rounded brachiole facets, and peripores more like those of *H. kiaeri* than *H. bratterudensis* (text-figs. 19B, 25). See text-figs. 4, 9 for range and geographic distributions.

Haplosphaeronis bratterudensis n. sp.

Plate 2, figs. 5-8; text-figs. 18C, D, 19A

1953 *Haplosphaeronis* cf. *kiaeri* Jaekel; Størmer, p. 84.

Diagnosis. A species of *Haplosphaeronis* with submerged diplopores, equally numerous all over the theca but missing on CO6 and CO7. Diplopores wide, usually lacking periporal wall, peripore below thecal surface. No tubercles and no calcified diplopore roofs.

Holotype. PMO 89201, preserved as an external mould (text-fig. 18C, D; Pl. 2, fig. 5).

Type horizon and locality. Lower Chasmops Shale containing *Neosaphus ludibundus* (*multidens* Zone); shore at Bratterud, Ringerike, Oslo Region.

Material. In addition to the holotype some twenty specimens are referred to this species from Ringerike and Asker.

Description. Theca: spherical, with a flat or concave base. The sides are gently curved. In most specimens the height of the theca is about equal to its width.

Plates: the plate surface between the diplopores is relatively smooth.

Diplopores: relatively large, usually parallel-sided or slightly elliptical, averaging 0.65×0.18 mm (text-fig. 25), and submerged below the plate surface. The periporal wall is low or not developed. The peripore width (pw_1) is significantly larger than in *H. kiaeri* (text-fig. 25; Pl. 2, figs. 7, 8), whereas the length does not differ to the same extent. In the basal area about five pores per mm^2 are present, whereas the number is five or six in the circum-oral plates.

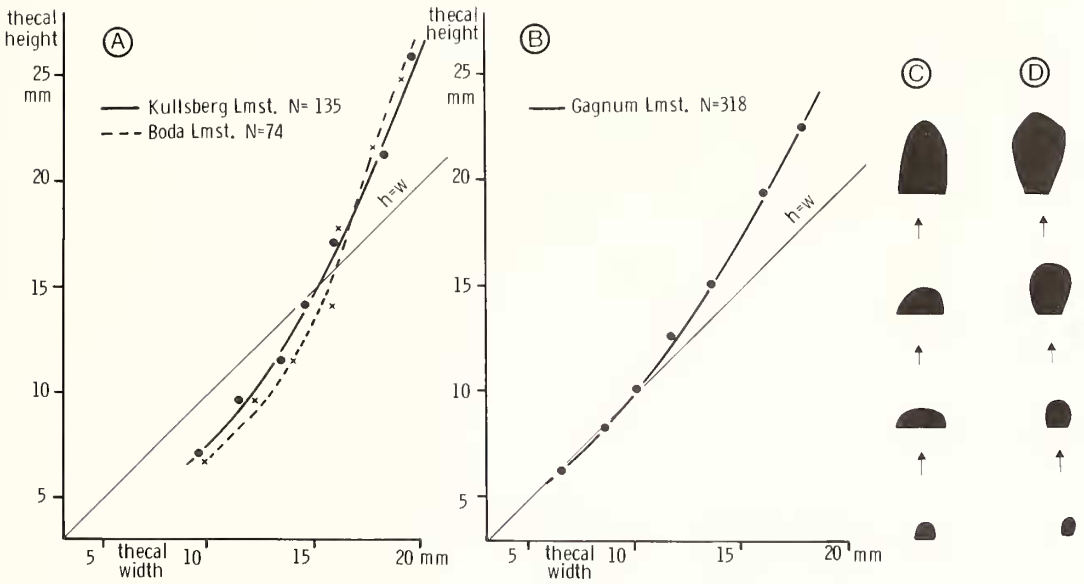
Peristome: the mouth is oval, the adanal side being almost straight in PMO 89202 (Pl. 2, fig. 6). The highest number of brachiole facets totals twenty-three. Most of the ambulacral furrows end in angular facets with deep incisions between them (text-fig. 19A). Commonly the first formed facets (see Bockelie 1978a, fig. 1) have rounded fringes, and later ones have more angular fringes (text-fig. 19A; Pl. 2, fig. 6). Individual facets are approximately 0.5 mm in diameter and are not as rounded as in *H. kiaeri*.

Periproct: adoro-lateral, oval to pyriform, and covered by an anal pyramid of five or six plates. The periproct lies about 1 mm below the oral margin. The anal pyramid is high, adorally inclined, and reaches almost to the level of the top of the palate (text-fig. 18D).

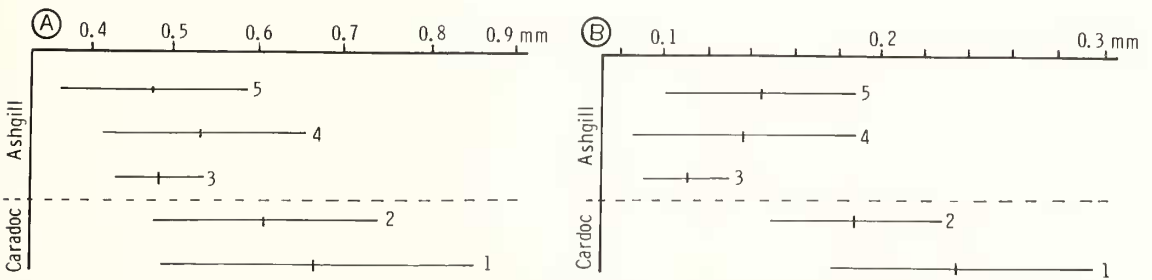
Gonopore: a relatively small circular pore, 1.5 mm in diameter, almost in contact with the first facet in radius I in the holotype.

Hydropore: a straight slit of variable length, adorally of the gonopore.

Attachment: direct, by an aboral attachment area, usually concave and about one-third to two-thirds the ambital diameter.



TEXT-FIG. 24. Thecal growth of *Haplosphaeronis oblonga* (Angelin) (A, C), and *H. kiaeri* Jaekel (B, D). All Swedish populations first produced a large basal surface ($h < w$), before attaining height. The points at which the growth gradients change may indicate the onset of maturity (see Bockelie 1978a). *H. kiaeri* has an equal growth rate both in height and width in young stages. Maturity in this particular population was reached at a thecal diameter of 10 mm after which the growth rate of thecal height increased ($h > w$). N, number of specimens in populations studied. Data arranged in size classes. C, D, ontogenetic changes in shape of the two species.



TEXT-FIG. 25. Peripore length (A) and width (B) of *Haplosphaeronis* species. A trend towards a decrease both in peripore length and width during the Ordovician is evident. 1, *H. bratterudensis* n. sp. (101 measurements); 2, *H. cf. kiaeri* Jaekel, Upper Chasmops Limestone (17–18 m level), Raudskjær, Asker (49 measurements); 3, *H. kiaeri* Jaekel, Gagnum Shale (5.5–6.0 m level), Tønnerud, Hadeland (120 measurements); 4, *H. kiaeri* Jaekel, Gagnum Limestone (21–22 m level), Tønnerud, Hadeland (88 measurements); 5, *H. kiaeri* Jaekel, Gagnum Limestone (27–28 m level), Tønnerud, Hadeland (80 measurements).

Remarks. *H. bratterudensis* differs from other *Haplosphaeronis* species (except some of the specimens referred to *H. oblonga* (Angelin) by Regnéll 1945) by the submerged position of the diplopores, and by the diplopores being almost as numerous in the basal portion as in the circum-oral plates. Some specimens from below the Kullberg Limestone of Sweden (figured by Paul 1972, pl. 6, fig. 1) are tentatively referred to *H. oblonga*. They are contemporary with the Norwegian *H. bratterudensis* and show similar structures. It is uncertain if these Swedish specimens should be referred to *H. bratterudensis*.

Genus *Eucystis* Angelin, 1878

Synonymy. *Proteocystites* Barrande, 1887; *Carpocystites* Oehlert, 1887; *Proteocystites* Bather, 1899; *Bulbocystis* Růžička, 1939.

Type species. *Eucystis raripunctata* Angelin, 1878, p. 31, from the Boda Limestone (Ashgill) of Osmundsberget, Dalarna, Sweden.

Diagnosis. A genus of Sphaeronitidae with pentagonal peristome; five ambulacra each with one or several food grooves terminating in ambulacral facets on circum-oral plates or somewhere on the thecal surface. Thecal plates arranged in three or more series and numbering twenty to fifty in total.

Remarks. As pointed out by Le Maître (1958, p. 304) and Prokop (1964, p. 30) a close relationship exists between *Eucystis* and *Bulbocystis*. *Bulbocystis* differs essentially in having a more regular arrangement of ambulacra (Kesling 1967, p. S242). I accept Le Maître's view and suggest a synonymy. Reed (1917, pl. 3, fig. 3, 3a) referred a specimen from Yunnan to *Eucystis* cf. *raripunctata*; the peristome is quadrilateral and each ambulacrum bears only one facet. To which genus Reed's species should be referred is uncertain. Paul (1973, p. 40) pointed out that several species of the rather variable *Eucystis* have stem-like projections formed by the basal plates, but no true stems are present. The Norwegian *Eucystis* species has a broad flat base.

Description. Theca: the shape and size of thecae of *Eucystis* species varies considerably. The largest species known is *E. barrandena* (Haeckel) which reaches 50 mm in height. Some species have a broad flat base, whereas others have stem-like projections of the basal plates; this may vary even within species.

Peristome: always pentagonal; those having a quadrilateral peristome which were formerly referred to *Eucystis* are now referred to a new genus, *Tetreucystis* n. gen.

Ambulacral system: five ambulacra are present, each with one or more facets at the end of short or long ambulacral furrows. New ambulacral furrows are added throughout life, in a manner typical of the family Sphaeronitidae (Bockelie 1978a); thus the total number of facets may not be a good taxonomic character. However, the distribution of ambulacral furrows in adults may at times be reliable at species level: one short furrow from each of the oral corners in *E. pentax* Paul, 1973; most facets present on the circum-oral plates in *E. angelini* Regnéll, 1945; and several facets below the circum-oral plates in *E. raripunctata* Angelin, 1878.

Periproct: the rounded, polygonal periproct is close to the mouth. It has ledges for insertion of plates; the aboral portion could open more than the adoral portion (text-fig. 26B, C). Neither oral nor anal plates have been found, and were probably very thin or more loosely joined to their relative openings.

Gonopore and hydropore: a circular gonopore and a slit-like hydropore are always present in positions typical for the Sphaeronitidae, the former across the suture CO7:CO1, and the latter across the suture CO6:CO1.

Plates: the plate arrangement varies in *Eucystis*: most species have only three plate series but *E. flava* has five or more. Only one generation of plates seems to be present. Details of the shapes of plate sutures within a species reveal considerable variation on one theme (text-fig. 26D-G). Such variations are more common in certain populations.

Diplopores: all plates are pierced by generalized diplopores with oval peripores but, as with other genera of the Sphaeronitidae, their width is less variable than their length and thus seems to be an important character for species discrimination. Covered diplopores have been found in individuals of some species.

Attachment: *Eucystis* was attached directly by an attachment area which differs in size from species to species. Some of the Swedish species have a small attachment area. No traces of an internal spine have been found.

Palaeoecology. *Eucystis* species from Norway occur in siltstones, presumably representing shallow water environments. They occurred, however, at greater depths than those containing rugose corals and seem to appear in environments of unstable sedimentation below wave base. The closely related

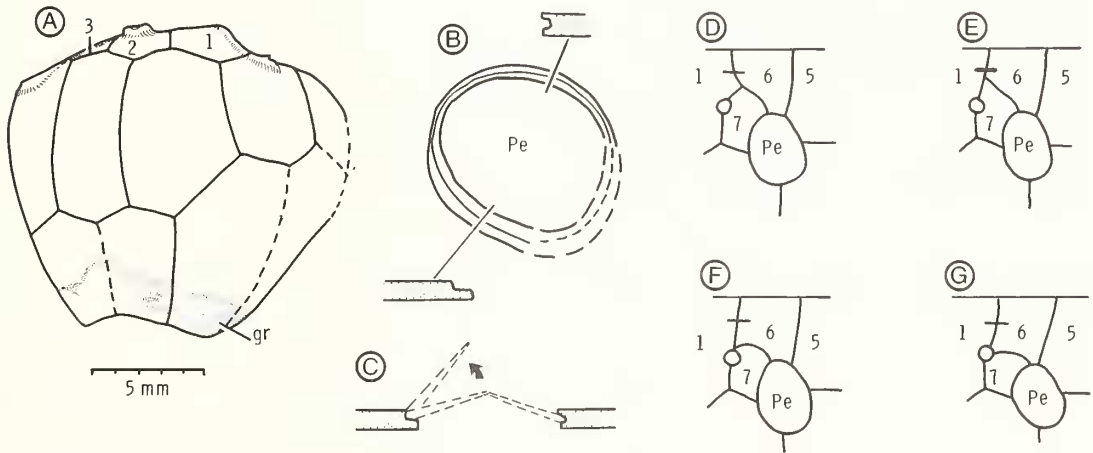
Tetreucystis n. gen. is rare in Britain (one species) and in Sweden (one species) but is not uncommon in Norway (three or four species). Ecological factors may have played some part in the distributional pattern of these genera. According to Paul (1973, p. 41) the number of ambulacral facets may exceed five in each of the British species where the total number is known. In the Swedish *E. angelini* the number of facets is fifteen to twenty, in *E. raripunctata* twelve to fifteen, and in the only Norwegian species five to seven. This may also reflect ecological conditions. The Swedish species may derive from more shallow water than both the Norwegian and British forms. Whereas a trend in the number of facets, as outlined above, can be observed in *Eucystis* species, the reverse trend occurs in *Haplosphaeronis* which lived in the same environments and which usually occur in the same beds as *Eucystis*. British *Haplosphaeronis* generally have more facets than Norwegian species, which in turn have more than Swedish species. As discussed elsewhere (Bockelie 1978a), ambulacral furrows and facets are added ontogenetically, probably to increase food-gathering capacity. It is possible that this increase also manifests itself phylogenetically; Devonian *Eucystis* species often have numerous and very long food grooves (Prokop 1964).

Regional distribution and stratigraphic range. Ashgill (upper Ordovician) of Sweden, Norway, Britain, Ireland, Bohemia, and ?Germany (*E. hercynica* Jaekel), Spain (Chauvel and Le Menn 1979); Devonian of Bohemia, France, Morocco, Algeria, and Central Sahara; so far totally unknown in the Silurian.

Eucystis langoeiensis n. sp.

Plate 5, figs. 5-8; text-figs. 26A, 27C, 32B

Diagnosis. A species of *Eucystis* with plates in three fairly regular circlets; in the lateral and basal plates the height exceeds the breadth ($x > y$); plates of the lateral series hexagonal. Circum-oral plates somewhat irregular in shape, but together forming a subcircular area. Diplopores not numerous; more common in the lateral than in the circum-oral plates; sparse or absent in the basal series. Five to seven ambulacral furrows and always one short furrow in radius II. Diplopores short (0.2 mm long) with faint periporal rim.



TEXT-FIG. 26. A, *Eucystis langoeiensis* n. sp., PMO 90947, holotype in lateral view showing plate configurations, some circum-oral plates (1, 2, 3), and irregular growth lines (gr) on basal plates, probably indicating that the specimen rested on the sea bottom during life. B, c, schematic view of periproctal opening (Pe) with a lower ledge, and an upper furrow for the insertion of periproctal cover plates; plates of the lower half were mobile whereas those of the upper half were not; this configuration is typical of *Haplosphaeronis* and *Eucystis*. D-G, *Eucystis angelini* Regn ll, from Sk lberget, Dalarna, Sweden; variations in the arrangement of circum-oral plates. CO6 always thins towards the periproct forming a pointed end; periproct surrounded by five plates. D, 56% of population; E, 11% of population; F, 22% of population; G, 11% of population.

Derivation of names. From Langøya, the type area.

Holotype. An almost complete specimen, PMO 90947 (Pl. 5, figs. 5, 8), from Langøya, Oslo, preserved as an external mould.

Horizon and localities. Top of Husbergøya Shale Formation (= uppermost part of Stage 5a), upper Ashgill, northern Langøya, south-western Rambergøy, western Gressholmen, and Husbergøya, Bunnefjorden, Oslo.

Material. Fourteen specimens in addition to the holotype.

Description. Theca: mostly globular with a height/width ratio close to one. Thecal diameter usually 12–15 mm. The base is broad, usually one-third to two-thirds the ambital diameter, and slightly concave.

Plates: three circlets of plates are present. The circum-oral plates are longer than wide. The CO6 : CO7 suture meets the CO1 : CO7 suture at the gonopore (seen in the holotype only). The hexagonal plates of the lateral and basal series are elongate. The lateral plate circlet contains nine plates, the basal circlet seven, and the circum-oral circlet always consists of seven plates. Fine 'growth' lines are present in the lowermost 2 mm of the basal plates of the holotype. These lines may indicate that the specimen lived with its base in the sediment (text-fig. 26A).

Diplopores: may be present on all plates, but are often sparse or absent in the basals. In CO1 to CO5, seven to ten diplopores were observed in each plate, but only two in CO6 and CO7. In the laterals there are usually two to three diplopores (five pores) per mm². On one plate (5 × 6 mm) twenty pores were counted. In the lateral series, diplopores are more numerous in the adoral than in the aboral part of the plates, and the long axes are more or less perpendicular to the plate margins, thus giving a radial arrangement. In PMO 92986 diplopores in the basal and lateral series are covered by a calcified diplopore roof. Peripore length: 0.42 ± 0.13 mm; peripore breadth: 0.21 ± 0.04 mm; length to breadth ratio: 0.09 ± 0.03 (mean ± 1 standard deviation, based upon forty-four measurements).

Peristome: measures 3.2 × 2.9 mm in the holotype; food grooves extend below the circum-oral plates. In radii II, III, and V one ambulacral side-branch occurs, whereas in radii I and IV there are two such branches. Two specimens, PMO 90877 and PMO 97139, each have five or six short ambulacral grooves and differ only slightly from other specimens of this species (Pl. 5, fig. 7).

Periproct: somewhat deformed in the holotype, but its original shape was probably subcircular, as can be seen from PMO 90872 where its diameter is about 3.6 mm.

Gonopore: at the upper left side of the anus with a diameter of approximately 1.5 mm.

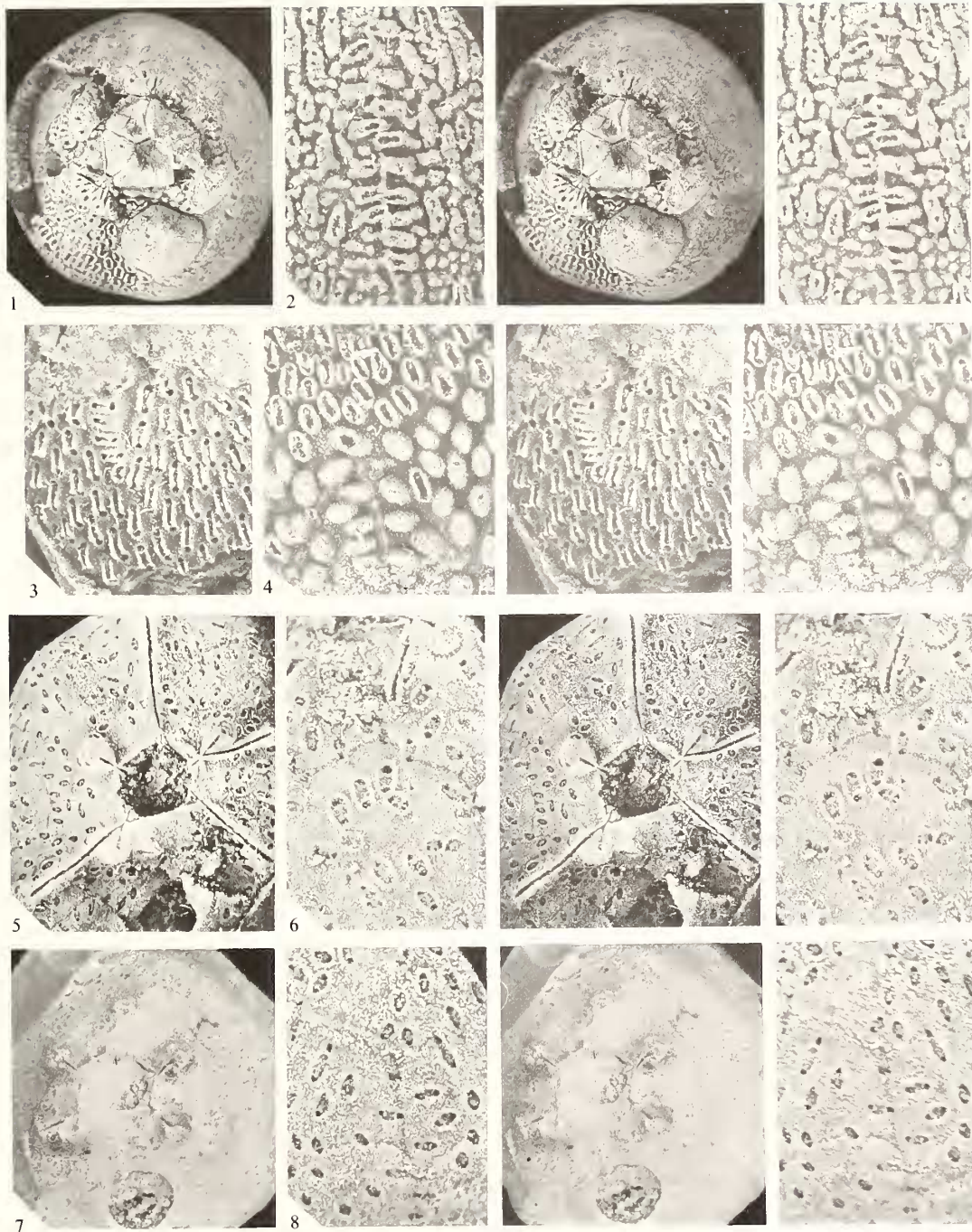
Hydropore: on a small ridge between the mouth and the anus, about 0.6 mm from the oral margin. The hydropore is bisected by the suture CO1 : CO6.

Remarks. *E. langøeyensis* differs from the British species in usually having more than one facet in each ambulacrum, and from the Swedish species in having fewer facets. It also differs from the other species by the shape of the circum-oral plates. It can be distinguished from the Devonian species of Bohemia by differences in facet distribution and surface ornament. Three species of *Eucystis* have been described from Sweden, i.e. *E. raripunctata*, *E. angelini*, and *E. acuminata*. A large number of specimens from the Riksmuseum, Stockholm, has been studied, resulting in some additional

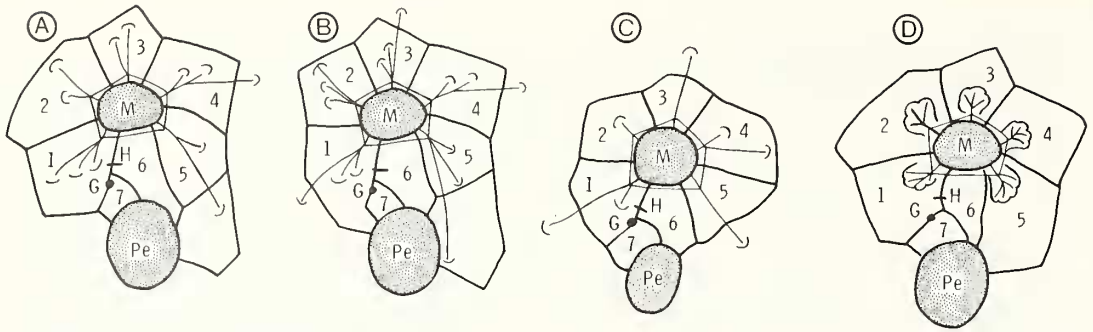
EXPLANATION OF PLATE 5

Figs. 1–4. *Haplosphaeronis kiaeri* Jaekel. Tonnerudodden, Hadeland. 1, PMO 79913, Gagnum Shale, × 4. 2, PMO 89920, cast showing details of pores on basal plate and suture (note that many pores are covered), Gagnum Shale, × 7. 3, PMO 90905, cast showing details of pores with development of spines on peripore wall in circum-oral plate, 21–27 m level, Gagnum Limestone, × 6. 4, PMO 90985, cast showing basal plate with covered pores in lower portion, open pores above and some pores partially covered, 31–32 m level, Gagnum Limestone, × 6.

Figs. 5–8. *Eucystis langøeyensis* n. sp. Upper part of Husbergøya Shale (Ashgill); 5, 6, 8, island off north-west Langøya, Oslo; 7, Gressholmen, Oslo. 5, PMO 90947, cast of holotype showing the continuation of food grooves into peristome border. (The number and position of ambulacral facets are characteristic of species), × 4. 6, PMO 90871, cast showing details of diplopores (note the large pores and peripore rims, and also the presence of some sutural pores), × 6. 7, PMO 97139, cast of young specimen with short ambulacra, × 3. 8, PMO 90947, cast of holotype showing details of diplopores at plate suture (note the faintly developed rim and some elongated peripores), × 6.



BOCKELIE, *Haplophaeronis* and *Eucystis*



TEXT-FIG. 27. Plate configuration of *Eucystis* species. A, B, two varieties of *E. raripunctata* Angelin showing differences in CO1 near periproct and differences in number and extent of ambulacral furrows (A, RM Ec 2376; B, RM Ec 2370, holotype). C, *E. langoyensis* n. sp., PMO 90947, holotype showing the relatively small number of facets in this species. D, *E. angelini* Regnéll with all facets close to the mouth (compiled from RM Ec 2056 and RM Ec 1938).

information concerning the plates of *E. raripunctata* and *E. angelini*, including a new diagram for plate configuration of *E. raripunctata* (text-fig. 27A, B) to replace that of Regnéll (1945, fig. 22.4). The holotype of *E. raripunctata* is somewhat abnormal in that CO1 is in contact with the anus (text-fig. 27B), and the ambulacral grooves of radius V are extremely long, reaching more than half-way down the side of the periproct. In all specimens of *E. raripunctata* studied, CO5 is never in contact with the anus, whereas this is the case with *E. angelini* (text-fig. 27D).

Genus *Tetreucystis* n. gen.

Synonymy. *Eucystis* (*partim*) auctores.

Type species. *Tetreucystis kalvoeyensis* n. gen., n. sp. from the Tretaspis Limestone (= Stage 4c β), lower Ashgill, Kalvoya, Oslo Region, Norway.

Diagnosis. A genus of Sphaeronitidae with quadrilateral peristome. Four branching ambulacra, one from each corner of the mouth. Theca composed of a limited number of polygonal plates in three or more series and numbering twenty to fifty.

Remarks. There is a distinct difference in the shape of the peristome of *Eucystis* and *Tetreucystis* n. gen. which I consider justifies the erection of the new genus for species possessing a quadrangular mouth. *Tetreucystis* n. gen. has a quadrilateral peristome like *Diplosphaeronis* Paul, but differs from the latter by having the periproct widely separated from the peristome, with more than three plates between the two orifices. At present five species can be assigned to *Tetreucystis* n. gen.; these include *T. munita* (Forbes, 1848), *T. quadrangularis* (Regnéll, 1945), *T. elongata* n. sp., *T. kalvoeyensis* n. sp., and *T. monobrachiolata* n. sp.

Description. *Tetreucystis* agrees in most respects with *Eucystis*, except in the shape of the oral area and that the ambulacral furrows seldom reach below the circum-oral circle (*T. quadrangularis* being the exception). Most *Tetreucystis* species have only one ambulacral furrow in each radius, but *T. kalvoeyensis* n. sp. has a total of eleven or twelve facets and *T. quadrangularis* twelve to sixteen facets. The general shape of the theca, the plate distribution, and type of pores are similar to *Eucystis*, apart from the rather elongated pores of *T. munita* and *T. elongata* n. sp.

Palaeoecology. *Tetreucystis* occurs in environments similar to those of *Eucystis* and in lithologies such as carbonate mud mounds (*T. quadrangularis* in Dalarna, Sweden), siltstones (*T. monobrachiolata* n. sp. on the islands in the vicinity of Oslo, Norway), and in nodular limestones (*T. munita* in

the Rhiwlas Limestone at Bala, North Wales; *T. kalvoeyensis* n. sp. and *T. elongata* n. sp. in the Bærum-Asker districts, near Oslo, Norway). *T. kalvoeyensis* and *T. elongata* seem to be mutually exclusive, one occurring in deeper water than the other (text-fig. 6C).

Regional distribution and stratigraphic range. Ashgill of Norway, Sweden, and Britain.

Tetreucystis kalvoeyensis n. sp.

Plate 6, figs. 1-4, 7; text-figs. 29C-E, 31A

Diagnosis. A species of *Tetreucystis* with theca composed of plates in five or six series, each individual plate varying in shape and size, being pentagonal or hexagonal. Circum-oral plates higher than broad ($x > y$). Diplopores usually numerous in the lateral and circum-oral plates, decreasing in number towards the basal portion of the theca and occasionally present even in the basal plates. Ambulacra often with three side-branches each, all confined to circum-oral plates. Total number of brachiole facets in adult specimens ten to twelve.

Holotype. An almost complete specimen, PMO 80030, preserved as an external impression (text-fig. 29C, E; Pl. 6, figs. 1, 3).

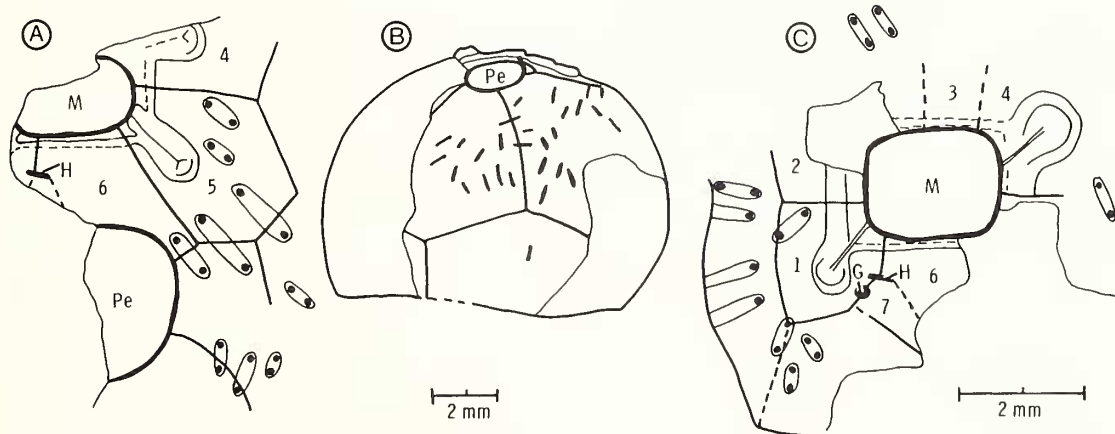
Type horizon. Tretaspis Limestone (= Stage 4c β), lower Ashgill.

Material. Over fifty more or less fragmentary specimens from Kalvøya (Bærum), Nesoya, Hvalstad, Raudskjær (Asker).

Description. Theca: variable in shape from spherical to inverted conical (text-fig. 29D, E). In the holotype, the height is 37 mm, the width 15 \times 13 mm.

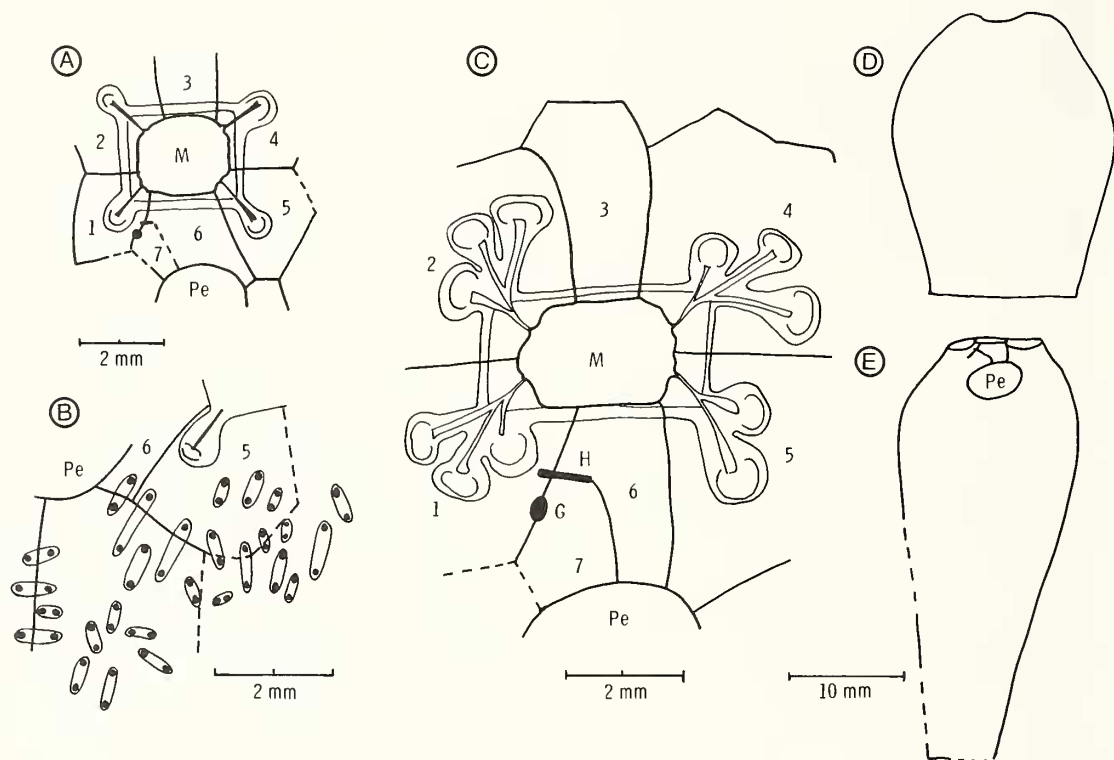
Plates: circum-oral plates are higher than broad; lateral plates vary in shape but are usually higher than broad. Eight or nine plates occur in the upper lateral series. In the oral region the sutures between CO7 and the adjoining lateral plates are not displayed. Thecal plates are about 0.6-0.8 mm thick. As in *T. elongata* n. sp., granular ornament occurs on the plates (also seen in well-preserved specimens of *Eucystis* and *Tetreucystis* from Sweden). The base of the theca is usually flat and may have served as an attachment area (text-fig. 29D, E).

Diplopores: occur in all thecal plates, the number decreasing towards the base, where the number of pores is two or three per mm², whereas in circum-oral and lateral plates it is five or six. A distinct radial arrangement of the diplopores is developed particularly in the two upper laterals. Peripore length: 0.54 \pm 0.09 mm; peripore width: 0.31 \pm 0.04 mm.



TEXT-FIG. 28. *Tetreucystis elongata* n. gen., n. sp. from Tretaspis Limestone, west side of Nesoya, Asker. A, PMO 91311, oro-anal area of holotype, showing right side of theca with circum-oral plates (4-6), mouth (M), hydropore (H), and periproct (Pe). B, lateral view of holotype showing some elongated diplopores. C, PMO 91312, oro-anal region. A, B, to same scale.

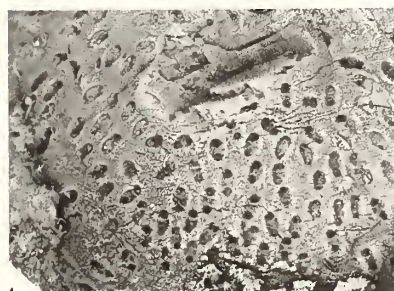
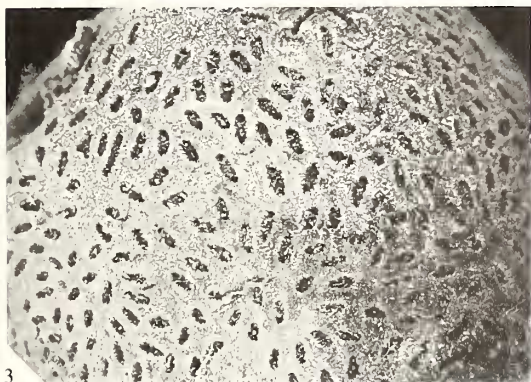
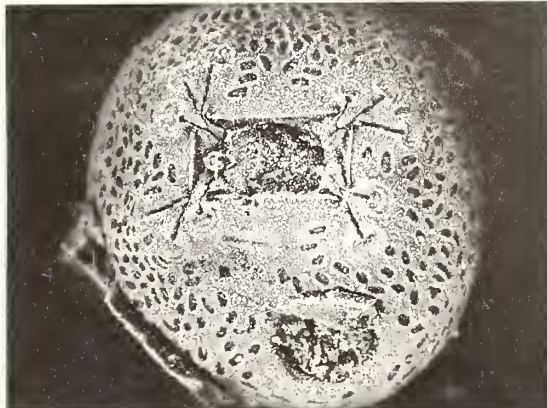
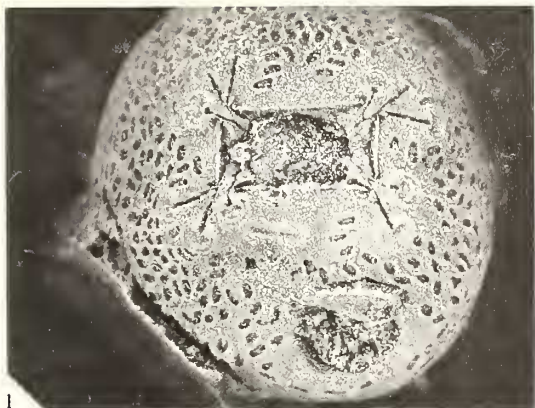
Peristome: slightly raised; the opening of the mouth is oval and the peristome border dips gently from the peristome down to the mouth. Grooves diverge from the ambulacral furrows before entering the mouth on the peristome border. The mouth is 4.2×2.5 mm. In the holotype three ambulacral side-branches occur in radii I, II, and IV, whereas only two occur in radius V. In PMO 90982 three side-branches occur in radii II and V but they cannot be counted in the other radii because of weathering. The side-branches never extend beyond the circum-oral plates. The anus is oval, 3.3×2.5 mm. Its long axis subtends an angle of 60° with the oral margin, and its adoral boundary lies 4.7 mm from that margin.



TEXT-FIG. 29. *Tetreucystis* n. gen. A, *T. elongata* n. sp., reconstruction of plate arrangement in the oro-anal area (cf. text-fig. 28). B, *T. elongata* n. sp., PMO 91311, holotype from Tretaspis Limestone, west side of Nesøya, Asker; diplopores (note their slight radial arrangement). C-E, *T. kalvoeyensis* n. sp. from Tretaspis Limestone, Kalvøya, Bærum. C, PMO 80030, holotype, reconstruction of plate configuration in the oro-anal area (note the somewhat elongated opening of the mouth, and food grooves leading on to a peristomal platform before entering the mouth); D, PMO 90981, lateral view showing shape of theca; E, PMO 80030, lateral view of holotype.

EXPLANATION OF PLATE 6

- Figs. 1-4, 7. *Tetreucystis kalvoeyensis* n. gen., n. sp. Tretaspis Limestone (lower Ashgill), Kalvøya, Bærum. 1, PMO 80030, cast of holotype, stereophoto of oro-anal region, $\times 5$. 2, PMO 90982, stereophoto of oro-anal area, $\times 5$. 3, PMO 80030, cast of holotype showing details of diplopores in lateral circling (note the radial arrangement of diplopores), $\times 7$. 4, PMO 90982, details of diplopores in circum-oral series, $\times 7$. 7, PMO 80022, outline of specimen with left side broken, $\times 3$.
- Fig. 5. *Eucystis raripunctata* Angelin. Boda Limestone (Ashgill), Östbjörka, Dalarna, Sweden. RM Ec 2370, holotype showing peripores of upper lateral series with granulated plate surface, $\times 6$.
- Fig. 6. *Tetreucystis elongata* n. gen., n. sp. Tretaspis Limestone (lower Ashgill), western side of Nesøya, Asker. PMO 91311, holotype in oral view. $\times 5$.



BOCKELIE, *Tetreucystis* and *Eucystis*

Gonopore: about 0.2 mm in diameter, occurs on the CO1 : CO6 suture and about 1 mm below the hydropore.
 Hydropore: 2 mm long and about 1 mm below the oral margin (text-fig. 29c).
 Attachment: direct by an aboral attachment area of variable size.

Remarks. *T. kalvoeyensis* differs from all other Norwegian *Tetreucystis* species in its larger number of brachiole facets. It differs from the contemporary Swedish *T. quadrangularis* in that the latter has more and longer food grooves, reaching down on to the lateral plates.

Tetreucystis elongata n. sp.

Plate 6, fig. 6; text-figs. 28, 29A, B, 31B

Diagnosis. A species of *Tetreucystis* with theca composed of plates in three regular circlets, the lateral plates having about equal height and breadth, whereas in the basal ones the height is less than the breadth. Diplopores elongate, about 1 mm long and 0.2 mm wide, more common in the lateral plates than in the circum-oral plates and sparse in the basal series. Brachiole facets small, 0.8 mm in diameter, close to mouth, never exceeding four.

Derivation of name. From the elongated shape of the diplopores.

Holotype. A somewhat imperfect specimen, PMO 91311 (text-figs. 28A, B, 29B, 31B; Pl. 6, fig. 6), showing only the right half of the theca (CO4–CO6) and in which neither the shape of most of the thecal plates nor the total plate number can be seen.

Type horizon. Tretaspis Limestone, lower Ashgill.

Material. Several more or less fragmentary specimens from Nesøya and Nesbru, Asker.

Description. Theca: hemispherical with flat base. The plate configuration of the theca is based upon only two specimens in addition to the holotype, PMO 91310 and 91312. Thecal height: 9–11 mm; greatest diameter: 11–12 mm. Maximum diameter of base equals the thecal diameter. Three plate circlets containing seven circum-orals, seven to eight laterals (eight in PMO 80083), and seven basals.

Plates: plate thickness is about 0.9 mm. Granulated surfaces are common, particularly in the circum-oral plates, as in Bohemian *Eucystis* (Prokop 1964). Laterals of equal length and breadth, the basals slightly shorter than wide.

Diplopores: occur in all three plate circlets, but are less common in the basals. In the latter, five pores were counted per mm²; in the circum-oral plates the number is only two or three. The diplopores are often arranged with their long axes perpendicular to plate margins. Diplopores long, but quite variable in length; some cross plate sutures (text-fig. 29B). Peripore length: 0.70 ± 0.17 mm; peripore width: 0.20 ± 0.04 mm. Ratio of peripore width to length: 0.14 ± 0.06 (mean ± 1 standard deviation, based upon fifty-four measurements).

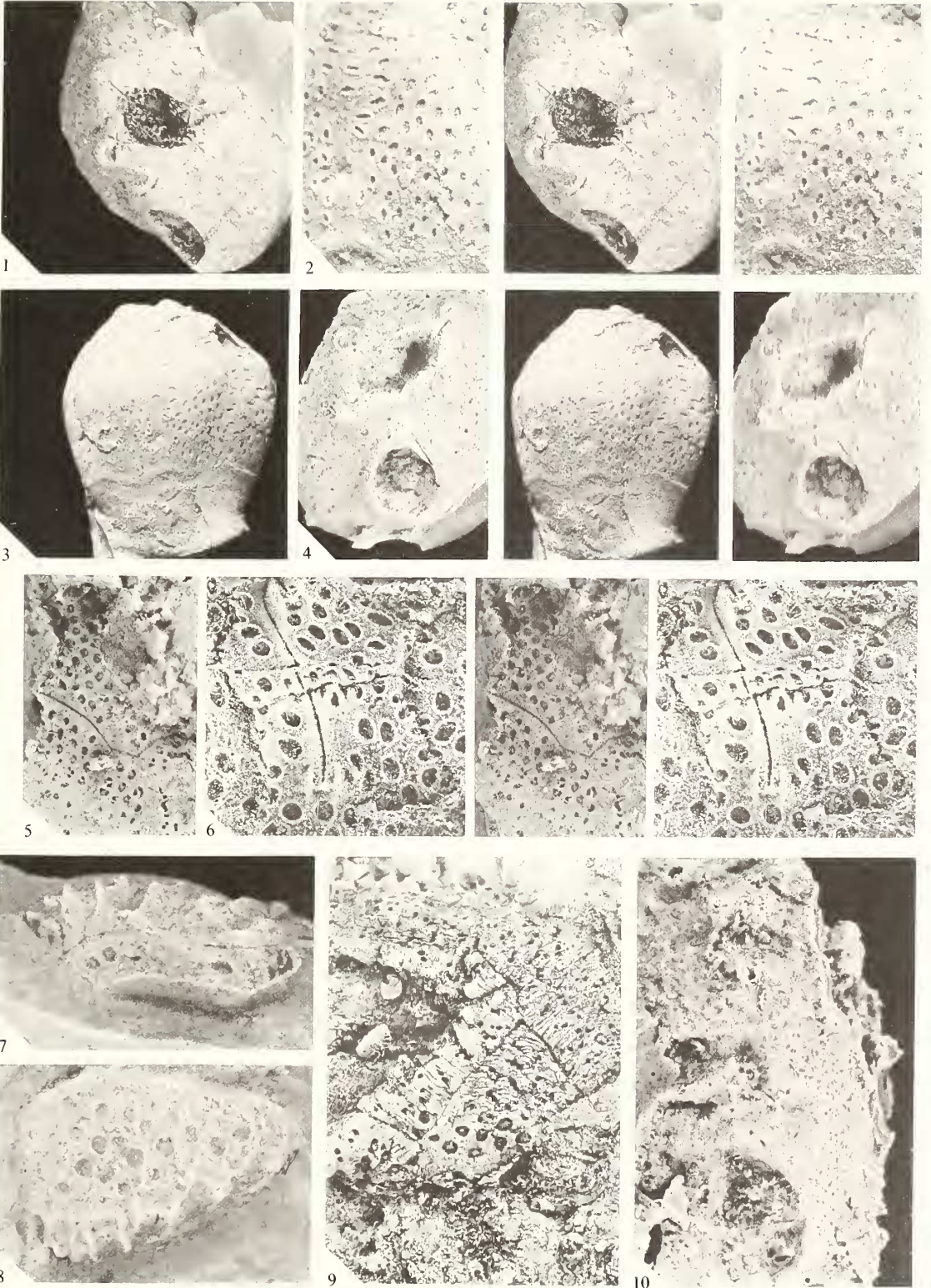
Peristome: measures 2.5 × 2.0 mm. The mouth is oval. Four ambulacra extend, one from each of the oral corners, to small brachiole facets about 1 mm from the oral corners.

EXPLANATION OF PLATE 7

Figs. 1–4. *Tetreucystis tetrabrachiolata* n. gen., n. sp. Husbergøya Shale (upper Ashgill); 1–3, Rambergøy, Oslo, and 4, north-west Langøya, Oslo. 1–3, PMO 92983, stereophotos of cast of holotype showing 1, oro-anal area, × 4; 2, diplopores in lower part of lateral plates, × 6; and 3, lateral view, × 2. 4, PMO 102.755, stereophoto of cast showing oro-anal area, × 4.

Figs. 5, 9, 10. *Pachycystis norvegica* n. gen., n. sp. Kalvsjø Formation (upper Ashgill), Kalvsjø Quarry, Lunner, Hadeland. 5, PMO 97103, stereophoto of cast of holotype showing diplopores on lateral series, × 4. 9, PMO 97141, part of theca with diplopores, × 6. 10, PMO 97103, cast of holotype showing quadrilateral peristome and large, circular anal area, × 5.

Figs. 6–8. *Sphaeronitid* indet. sp. A. Husbergøya Shale (upper Ashgill); 6, Skogerholmen, Asker, and 7, 8, Ostøya, Bærum. 6, PMO 90264, stereophoto of cast showing ambulacrum and diplopores, × 4. 7, PMO 97105, cast showing circum-oral plates with branching ambulacra seen from above, × 5. 8, PMO 97105, cast showing circum-oral plate seen in lateral view, showing diplopores, × 5.



BOCKELIE, *Tetreucystis* and *Pachycystis*

Periproct: slightly ovate with its long axis perpendicular to the oral margin. It measures 2.5×1.8 – 2.0 mm with the adoral boundary 1.3 mm below the oral margin (in PMO 91311).

Gonopore: 0.25 mm diameter, set just below the hydropore and close to the brachiole facet in radius I.

Hydropore: occurring less than 0.5 mm from the oral margin. It is bisected by the CO1:CO6 suture (text-fig. 28c).

Remarks. *T. elongata* differs from most other *Tetreucystis* species in the characteristic shape of its diplopores. It resembles *T. munita* (see Paul 1973) but differs in that the diplopores of *T. munita* are shorter (0.54 mm) than in *T. elongata* (0.70 mm), the mouth frame of *T. munita* is elevated on the thecal surface, and the diameter of the brachiole facet in *T. munita* is almost twice that of *T. elongata*.

Tetreucystis tetrabrachiolata n. sp.

Plate 7, figs. 1–4; text-figs. 30, 31c

Diagnosis. A species of *Tetreucystis* with theca composed of plates in three circlets, lateral plates higher than wide. Diplopores rounded, common in the circum-oral plates. Brachiole facets 1.3 mm in diameter. The number of facets rarely exceeds four.

Derivation of name. The name alludes to the almost constant number of brachiole facets, one in each of the oral corners.

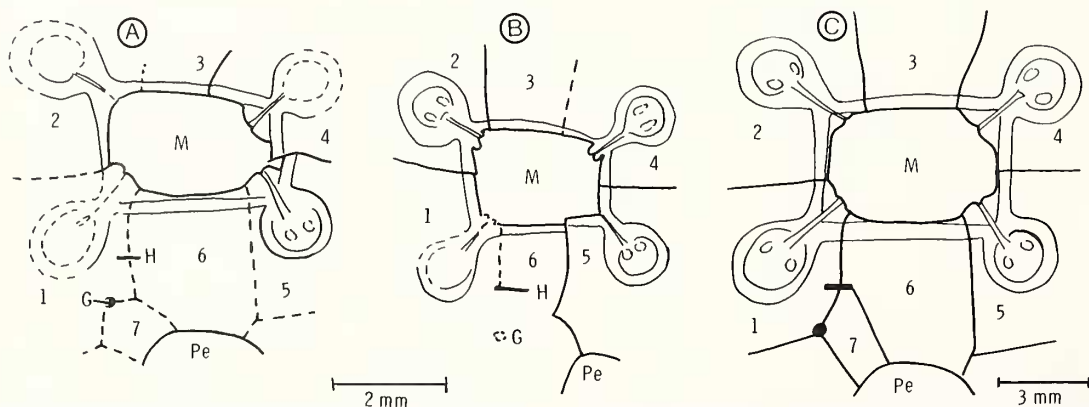
Holotype. A somewhat compressed specimen, PMO 92983, preserved as an external mould (Pl. 7, figs. 1–3). Only two-thirds of the theca is visible; some lateral and basal plates are not preserved.

Type horizon. Husbergøya Shale Formation, upper Ashgill, Rambergøy, Bunnfjorden, Oslo.

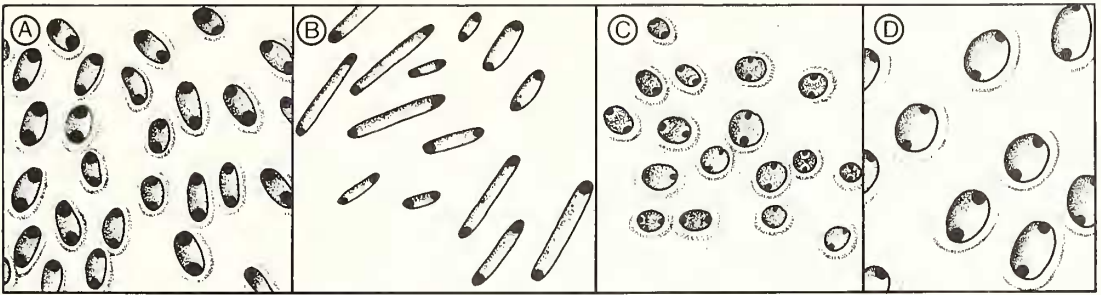
Material. In addition to the holotype, ten specimens from several of the islands in the Oslo district.

Description. Theca: globular with flat or slightly concave base. The plate configuration cannot be seen clearly in all specimens, partly due to cracks that confuse the issue. A composite reconstruction is made in text-fig. 30c. The theca consists of three series of plates, including seven circum-orals, eight laterals, and seven or possibly eight basals. Thecal height 13–20 mm; thecal diameter about two-thirds of thecal height. In most specimens the base is about one-third the thecal diameter but in some the base is slightly prolonged. In such cases the diameter of the base may be 5×7 mm (PMO 92991) or 5×8 mm (in the holotype).

Plates: approximately 1 mm thick. The plate surface is smooth. Both laterals and basals are higher than broad, whereas in the circum-orals the height and breadth is the same.



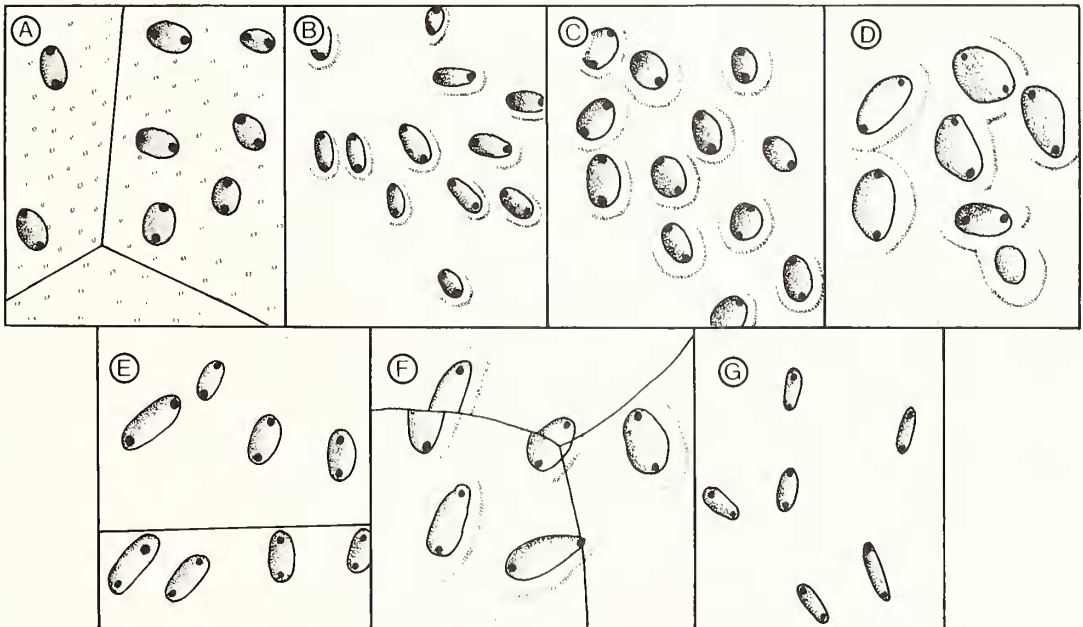
TEXT-FIG. 30. *Tetreucystis tetrabrachiolata* n. gen., n. sp. Plate distribution of oro-anal region. A, PMO 90890, Husbergøya Shale, south-west Rambergøy, Oslo. B, PMO 90873, Husbergøya Shale, north-west Langøya, Oslo. C, reconstruction. M, mouth; G, gonopore; H, hydropore; Pe, periproct.



TEXT-FIG. 31. Diplopores of *Tetreucystis* n. gen. A, *T. kalvoeyensis* n. sp., PMO 80030, holotype, Tretaspis Limestone, Kalvoya, Bærum. B, *T. elongata* n. sp., PMO 91311, holotype, Tretaspis Limestone, Nesoya, Asker. C, *T. tetrabrachiolata* n. sp., PMO 92983, holotype, Husbergoya Shale, Rambergøy, Oslo. D, *T. quadrangularis* (Regnéll), RM Ec 2119, Boda Limestone, Dalarna, Sweden (original of Regnéll 1945, pl. 14.2).

Diplopores: present all over theca, but most common in the circum-oral plates, where six to seven pores per mm^2 occur. In the lateral plates the number is four or five and in the basals only three or four. In some specimens the basals are devoid of diplopores. There is a tendency towards a radial arrangement of diplopores. Peripore length: 0.31 ± 0.10 mm; peripore width: 0.18 ± 0.02 mm. Ratio of peripore length to peripore width: 0.70 ± 0.02 (mean ± 1 standard deviation, based upon twenty-four measurements).

Peristome: 4.2×3.2 mm in the holotype, but the proportions may vary (in PMO 92984, 4.5×2.0 mm). In most specimens four ambulacra extend, one from each of the oral corners, just on to the circum-oral plates. In PMO 90896 two facets have been found in radius I.



TEXT-FIG. 32. Diplopores of *Eucystis* species. A, *E. varipunctata*, RM Ec 2370, holotype, Boda Limestone, Östbjörka, Dalarna, Sweden. B, *E. langoeiensis* n. sp., PMO 90947, holotype, Husbergoya Shale, north-west Langoya, Oslo. C, *E. angelini*, RM Ec 1974, Boda Limestone, Dalarna, Sweden. D, *E. globula*, SM A7800, holotype, Ashgill Shales (Paul 1973, text-fig. 27C). E, *E. acuminata*, RM Ec 2173, holotype, Boda Limestone, Gulleråsen?, Dalarna, Sweden. F, *E. libernica*, BM(NH) E28758, Kildare Limestone (Paul 1973, text-fig. 27D). G, *E. pentax*, SM A74802, Ashgill Shales (Paul 1973, text-fig. 27F). All approximately $\times 10$.

Periproct: subcircular with a diameter of 3.1 mm in PMO 90890.

Gonopore: below the hydropore and nearer the brachiole facet of radius I than the anus.

Hydropore: on a slightly elevated ridge, 1.4 mm below the peristome border and bisected by the CO1 : CO6 suture.

Remarks. *T. tetrabrachiolata* n. sp. is the only species of the genus occurring in the Husbergøya Shale. The contemporary Swedish *T. quadrangularis* can readily be distinguished from the Norwegian species by the presence of many more brachiole facets, and longer food grooves, reaching down into the lateral plates. *T. tetrabrachiolata* is separable from *T. kalvoeyensis* by the latter's larger number of brachioles. *T. tetrabrachiolata* is distinguishable from *T. elongata* by the shape of the diplopores and the shape of the lateral plates. It differs from *T. munita* in the shape of the pores, those of the latter being elongate.

Genus *Archaegocystis* Jaekel, 1899

Synonymy. *Pyrocystites* Barrande, 1887 (pars).

Type species. *Pyrocystites desideratus* Barrande, 1887, p. 170, by original designation of Jaekel, 1899, p. 395; Sárka Beds (Llanvirn), Osek, Bohemia.

Diagnosis. A genus of Sphaeronitidae with globular to spherical theca; plates more or less randomly arranged; ambulacra short, confined to peri-oral plates, branching fan-wise with three to seven facets each; diplopores oval to elongate with or without narrow unspecialized peripore rims and usually randomly orientated.

Archaegocystis cf. *granulata* Paul, 1973

Plate 3, figs. 7, 9

Material. One specimen, PMO 97106.

Horizon and locality. Ashgill; Sørbakken Limestone, Frognoya, Ringerike, Oslo Region.

Description. One sagittally divided half theca. Two ambulacra are preserved but the mouth, anus, gonopore, and hydropore are missing. Thecal height 26 mm; thecal diameter 22 mm. Attached directly by aboral circular attachment area, 3.5 mm in diameter.

Plates: total number unknown, but approximately five plate circlets present. Plates of slightly variable size, the largest reaching approximately 6-7 mm. Most (possibly all) plates have diplopores arranged radially (Pl. 3, fig. 7). Plate surface covered with fine granular ornament and faint peripore rims.

Diplopores: with simple peripore rims, often strongly developed, but in several cases weak or almost missing. Oval to elongate, rarely extremely elongate as in *A. stellulifera* (Salter). Length 0.25-2.0 mm (average 0.65 mm); width 0.18-0.40 mm (average 0.32 mm); averages based on thirty-four measurements.

Peristome: not present. Outermost portions of food grooves are present, forming small knobs. Food grooves were probably short, reaching to the centre of the circum-oral plates only.

Periproct: unknown.

Gonopore and hydropore: unknown.

Attachment: direct, by circular aboral attachment area with a diameter of 3.5 mm.

Remarks. This specimen shows most similarities with *A. granulata*. The lack of information about the oral area makes the determination slightly uncertain. The mean values of diplopore lengths and widths are not very different from those of British material (0.79 mm and 0.31 mm respectively). The granular surface ornament of the Norwegian specimen is also very similar to that of the British form. The characteristic surface granulation clearly distinguishes *A. granulata* from *A. stellulifera* (Paul 1973, p. 39). Some differences exist both in the shape and in the ornament between the British and Norwegian forms. However, because no complete specimen has yet been found in Norway, a new species is not erected.

Sphaeronitidae sp. A

Plate 7, figs. 6-8; text-fig. 33f

Material. One partial theca, PMO 90264, and two circum-oral plates, PMO 97105 and PMO 97140.

Horizon and localities. Husbergoya Shale Formation, Skogerholmen, and Ostoya, Bærum, Oslo Region.

Description. About one-third of the theca is preserved; it may have been about 40 mm high \times 26 mm wide. Only part of the upper surface remains. The theca tapers slightly towards the base, with an oval attachment area originally about 20 \times 15 mm. Base concave. Two series of roughly hexagonal thecal plates are preserved, but as many as four or five may have been present. Thecal plates have a granular ornament. The shape of the peristome is unknown. Food grooves of possibly two radii are preserved, representing radii II and III, or III and IV. In one of these radii two branching ambulacra can be seen, one of which reaches below the circum-oral circlet. The two individual circum-oral plates contain five to six side-branches off one main food groove. This main groove is parallel to the nearest plate suture. The brachiole facets are unlike those of any other Norwegian cystoid, but show similarities *inter alia* to the facets of *Craterina*.

Diplopores: numerous in the upper portion of the theca of PMO 90264. The diplopores are subcircular in outline and provided with a thick peripore wall. Mean diplopore length 0.71 mm; mean width 0.50 mm; length to width ratio 1.46 (based on thirty-seven measurements). No traces of mouth, anus, gonopore, or hydropore.

Palaeoecology. Found in a shallow water siltstone sequence extending for about 10 \times 10 km, with abundant echinoderms, bryozoa, and brachiopods. The brachiole facets indicate the presence of delicate brachioles, and the animals thus may have lived in clear water with moderate sedimentation rates.

Remarks. No described cystoid is directly comparable to this species. However, it is clearly a sphaeronitid from the type of food grooves and diplopores. To some extent it resembles *Eucystis*, *Archaegocystis*, and *Craterina*, but most likely represents a new genus.

Family PARASPHAERONITIDAE n. fam.

Diagnosis. A family of Sphaeronitida with a relatively large quadrilateral peristome, surrounded by eight peri-oral plates. The margin of the peristome is pierced by a large number of small pits; diplopores are complex. Four ambulacra, each leading to one large brachiole facet; periproct large, not very far down on the theca.

Remarks. Parasphaeronitidae is erected for two genera, *Parasphaeronites* n. gen. and *Pachycystis* n. gen. It is separable from the Sphaeronitidae by the presence of eight peri-oral plates. The family resembles the Holocystitidae in the number and distribution of peri-orals, but differs in having diplopores. Parasphaeronitidae differ from the Aristocystitidae in the shape of the peristome, which in the latter family has two broad ambulacral tracts which meet at a small ovate mouth (see Paul 1973, p. 57).

The Parasphaeronitidae seem to represent a transition between the Sphaeronitidae and the Holocystitidae, at least as far as the oral area is concerned. The humatipores of the holocystitids are known only from their exterior appearance (at the outer portion of the thecal plates) and the connections of canals through their plates are not known. In *Parasphaeronites* the canals are extremely complicated and show patterns not unlike those of the Aristocystitidae. The Parasphaeronitidae thus may also show some similarities to the Aristocystitidae, as far as the internal portions of the pore-structures are concerned. The Parasphaeronitidae at present contains two genera only, and both occur in the upper Ordovician (Ashgill) Kalvsjø Formation (= Stage 5a) and an unnamed formation from Ringerike (= Stage 5b) (Hirnantian), of the Oslo Region, Norway.

Genus *Parasphaeronites* n. gen.

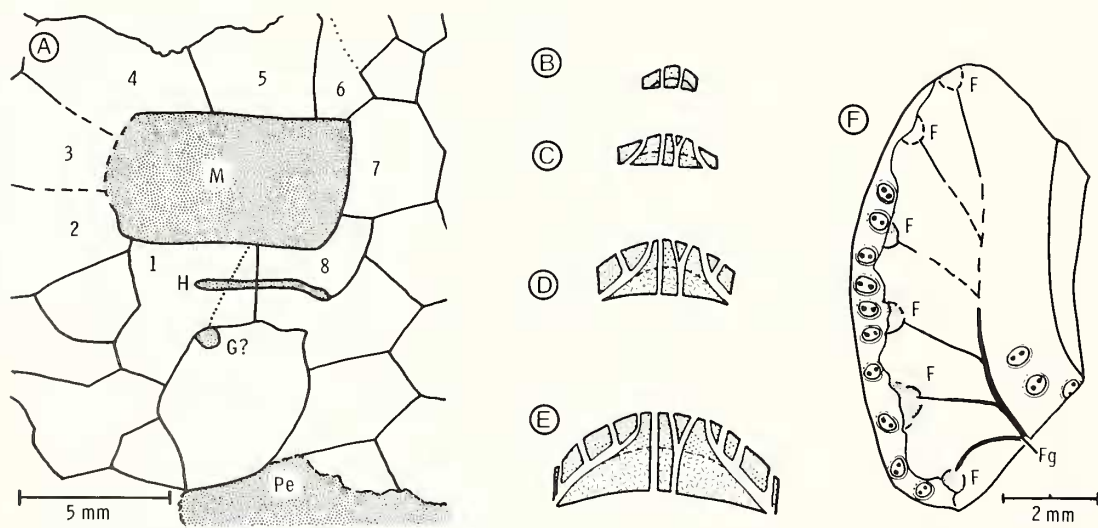
Synonymy. See *Parasphaeronites socialis* n. sp.

Type species. *Parasphaeronites socialis* n. gen., n. sp.

Diagnosis. A genus of Parasphaeronitidae with large globular theca composed of numerous irregular plates, with elevated plate centres forming irregular external surface; pores relatively close together with broad peripore rim, giving the appearance of *Sphaeronites*. One large ambulacral facet at each of the four oral corners. Periproct separated from the mouth by two plates.

Remarks. *Parasphaeronites* does not resemble any known cystoid. The presence of eight peri-orals and diplopores clearly distinguishes it from all others. The diplopores show similarities to both the Aristocystitidae and the Sphaeronitidae. *Parasphaeronites* is known from one species only, *P. socialis* n. sp. It differs from *Pachycystis* n. gen. in the arrangement of thecal plates around the peristome, the position of the periproct, the location of the gonopore, and in the more simple type of diplopores in the latter genus.

Description. The theca is globular, usually 40–50 mm in diameter, and consists of at least forty to fifty plates. The base is concave and irregular. The precise plate arrangement cannot be worked out easily, because the numerous specimens are usually crushed together and the thecae generally weather more rapidly than the matrix. The stereom of the thecal plates is often well preserved and shows an inner coarse mesh and an outer fine mesh structure. The pore structures are very well preserved, showing a rather complex pattern of canals through the plates. Three types of canals occur: (1) canals leading right through the plate from simple pores or a diplopore; (2) Y-shaped canals leading to two different diplopores; and (3) a main canal of low angle giving off several side-canals, each of which leads to a different diplopore (text-figs. 12F, 33B–E; Pl. 8, figs. 3, 6, 7). The periproct is situated some way down the theca and is separated from the mouth by one plate in addition to the peri-orals. The



TEXT-FIG. 33. A, *Parasphaeronites socialis* n. gen., n. sp. PMO 90974, holotype showing plate configuration of oro-anal area (drawing reversed in relation to specimen which is probably seen from inside); the quadrilateral mouth (M) is surrounded by eight peri-oral plates (1–8); hydropore (H), possibly gonopore (G?) and periproct (Pe) visible. B–E, *P. socialis* n. gen., n. sp., schematic representation of plate growth and additions of simple and complex canals; notice that the complex canals (branched) occur at the boundary between the fine mesh layer (dotted) and the coarse mesh layer (irregularly hatched); simplified. F, *Sphaeronites* indet. sp. A., PMO 97105, Husbergoya Shale, V. Ostoya, Bærum, circum-oral plate showing food groove (Fg) with six side-branches and facets (F), and diplopores on the side.

shape of the periproct is difficult to establish, but it seems to be as large as the peristome. The hydropore is a long slit-like opening crossing the sutures PO1 : PO6. The gonopore is located somewhat lower down on the theca and at the left side of the hydropore-periproct line. Attachment was direct, with a slightly concave base.

Palaeoecology. *Parasphaeronites* has been found in only one locality where it is extremely common, filling erosion channels in a reef.

Parasphaeronites socialis n. sp.

Plate 8, figs. 1, 3, 5-7; text-fig. 33A

1897 *Sphaeronites* sp.; Kær, p. 17.

1948b *Sphaeronites* sp.; Regnéll, p. 35.

Diagnosis. A species of *Parasphaeronites* with numerous thecal plates, not arranged in definite circlets; plates thick with elevated centres; diplopores present on most of the thecal plates, numerous, peripore with distinct rims, peripore length 0.5-0.6 mm.

Holotype. PMO 90974, a specimen showing the oro-anal area from the inside (text-fig. 33A; Pl. 8, fig. 1).

Material. In addition to the holotype, more than a hundred specimens.

Horizon and locality. Upper Ashgill; within channels in the reef of an unnamed formation, Ullerntangen, Ringerike, Oslo Region.

Description. As for the genus. The holotype shows the inside of the theca (Pl. 8, fig. 1); the plate diagram (text-fig. 33A) is reversed to show the external plate configuration.

Plates: one or possibly two generations in some parts of the theca. Four plate circlets at least in the holotype. Plates mostly elongated in oral-aboral direction. Most plates 6 × 4 mm. A circlet must have consisted of ten to fifteen plates; the basal circlet probably consisted of ten plates. Plate thickness 1-2 mm.

Respiratory pores: 0.54 × 0.33 mm with broad low periporal rim, or rimless peripores. Diplopores numerous all over the thecal surface including the basal plates, but absent near plate sutures. Some haplopores may be present. The canals within the plates are very complex (text-figs. 12F, 33B-E; Pl. 8, figs. 3, 6, 7).

Peristome: 8.1 × 4.4 mm, surrounding oval mouth. Small pits present on the peristome border resemble those of holocystitids (Paul 1971).

Periproct: the shape cannot be made out but it is about 7 mm from the lower border of the peristome frame.

Gonopore: circular, 0.48 mm in diameter.

Hydropore: present 1.2 mm below the peristome frame.

Remarks. *P. socialis* has pore structures resembling those of *Sphaeronites* on its external surface. The numerous pores all over the theca give it a high respiration potential, and in this respect it also resembles *Sphaeronites*. The complex pattern of pore canals within the thecal plates makes it one of the most difficult cystoids in Norway to study with respect to the peripore connections. However, it can be demonstrated that individual canals led to a peripore and that a complex circulatory system existed.

Pachycystis n. gen.

Type species. *Pachycystis norvegica* n. gen., n. sp., by monotypy.

Type horizon and locality. Kalvsjø Limestone, upper Ashgill; Kalvsjø, Hadeland, Oslo Region.

Diagnosis. A genus of Parasphaeronitidae with quadrangular peristome surrounded by eight peri-oral plates. Four ambulacra, each terminating in a large facet close to the mouth. A large periproct set closely to the peristome. Thecal plates numerous and irregular. Diplopores very common in the oral area, diminishing in number towards the base where they are absent. Directly attached by a slightly concave base.

Remarks. *Pachycystis* differs from *Parasphaeronites* by the periproct being close to the peristome border in the former, and separated by two plates in the latter. The gonopore of *Pachycystis* borders

PO1 and the peristome, whereas in *Parasphaeronites* the gonopore is located closer to the peristome. Thecal plates of *Pachycystis* are gently elevated, but strongly tumid in *Parasphaeronites*.

Description. The theca is sack-like with plates of different shape, often elongated, pentagonal, or hexagonal. No complete specimens exist, and thus the size cannot be clearly established. Total height of the theca seems to be in the range of 40–50 mm and diameter of 25–30 mm. PO1, PO3, PO5, and PO7 each contain one large brachiole facet, almost circular and 2.5–3.0 mm in diameter. Two muscle scars, both elongate, occur in each of the facets. The mouth may have been covered in life by a palate, but it has not been observed. A slit-like hydropore is present on PO1 and ends at the PO1:PO8 suture. A possible gonopore is located at the upper left side of the periproct, and is 0.6 mm in diameter. A large slightly ovate periproct, 7.5 × 5.5 mm, is set close to the lower margin of the mouth frame and is bordered by PO1, PO7, and PO8.

Diplopores are numerous in the upper half of the theca, usually 0.4 × 0.3 mm. They are densely packed in the circum-oral portion of the theca (four or five per mm²) but become reduced in number towards the base, where pores are absent. The long axis of the pores do not seem to show any preferred orientation. *Pachycystis* was attached directly by an attachment area which was slightly concave. Its diameter may be in the order of 20 × 20 mm from the general appearance of the theca, but has been found to be 5 × 3 mm in one specimen.

Palaecology. *Pachycystis* has been found only on the flanks of a mudbank at Kalvsjø, Hadeland, where it is preserved in a calcareous shale.

Pachycystis norvegica n. sp.

Plate 7, figs. 5, 9, 10; text-fig. 34A, B

Diagnosis. As for the genus.

Holotype. PMO 97103, an external mould of the oral area (text-fig. 34A; Pl. 7, figs. 5, 10).

Horizon and locality. Upper Ashgill; Kalvsjø Formation, mud bank, Kalvsjø, Hadeland, Oslo Region.

Material. Holotype, PMO 97141 and PMO 101.835, and two moulds, PMO 97102 and PMO 97104.

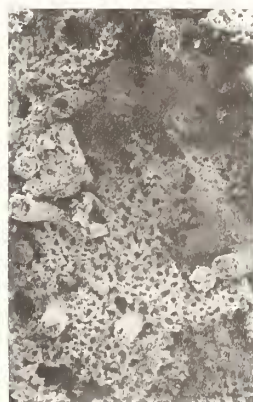
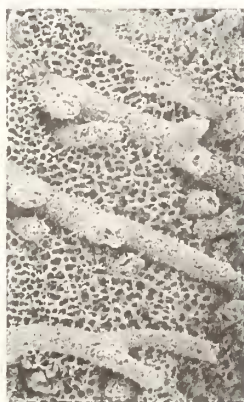
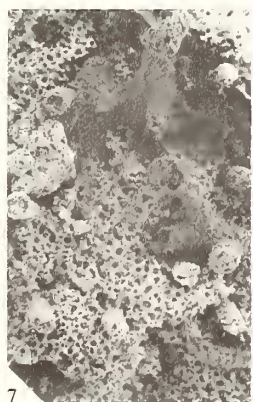
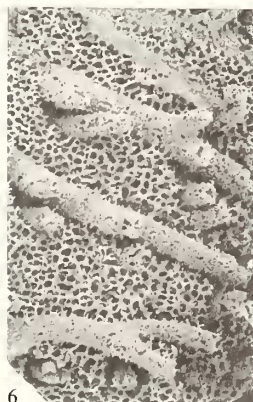
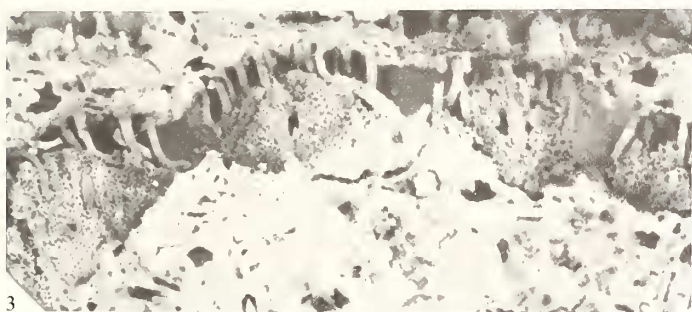
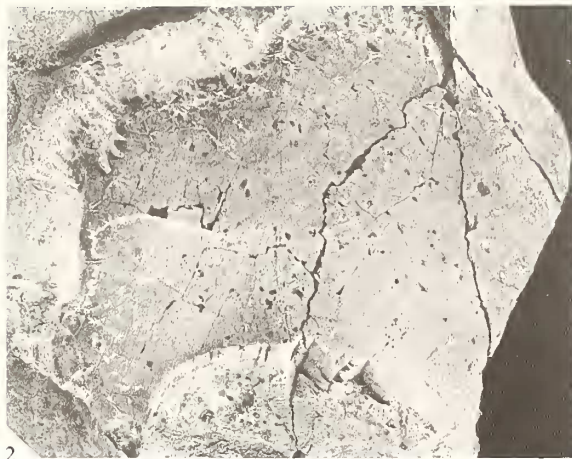
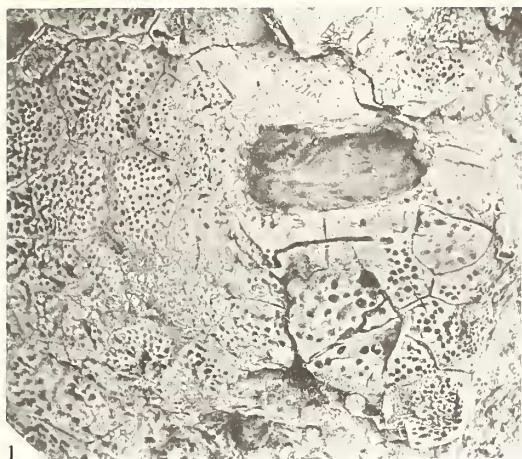
Description. As for the genus. In addition some measurements have been made on the sizes of diplopores. The peripores are slightly elongated with fairly large pores. Some of the peripores close to the plate sutures are smaller than those elsewhere, probably indicating that new pores are formed close to sutures. Peripore length 0.35–0.50 mm; width 0.25–0.40 mm (text-fig. 34B). Attachment was direct with a small elongate attachment area (5 × 3 mm in PMO 101.835).

EXPLANATION OF PLATE 8

Figs. 1, 3, 5–7. *Parasphaeronites socialis* n. gen., n. sp. Unnamed formation (Hirnantian), Ullerntangen, Ringerike. 1, PMO 90974, holotype, oro-anal area seen from inside (?) of theca (specimen strongly weathered). 3, PMO 105.707, etched specimen showing details of canals in sagittal view; the fine stereom layer (outer) is dissolved, the inner coarse mesh layer filled with asphalt (note how the canals parallel the surface of the coarse mesh layer), × 10. 5, PMO 55533, stereophoto of strongly convex plates with pores, × 5.5. 6, PMO 105.715, SEM stereophoto showing details of complex canals with main canals and side branches towards edge of plate (SEM 2362/61), × 20. 7, PMO 105.715, SEM stereophoto showing details of complex canals towards plate centre (note vertical position of canals as opposed to low angle canals at plate edge) (SEM 2356/57), × 20.

Fig. 2. *Incertae sedis* sp. A. Upper Chasmops Limestone (12.1 m below top), Raudskjær, Asker. PMO 103.320, basal portion of theca with minute diplopores, × 2.

Fig. 4. *Incertae sedis* sp. B. Encrinite Limestone (2 m above base, within lowermost portion of reef), Steinvika, Langesund. PMO 105.836, basal portion of a theca showing small diplopores, × 3.



BOCKELIE, *Parasphaeronites* and *Incertae sedis*

Incertae sedis sp. A

Plate 8, fig. 2

Material. One specimen, PMO 103.320.

Horizon and locality. Upper Caradoc; Upper Chasmops Limestone, 12.1 m below the top, Raudskjær, Asker, Oslo Region.

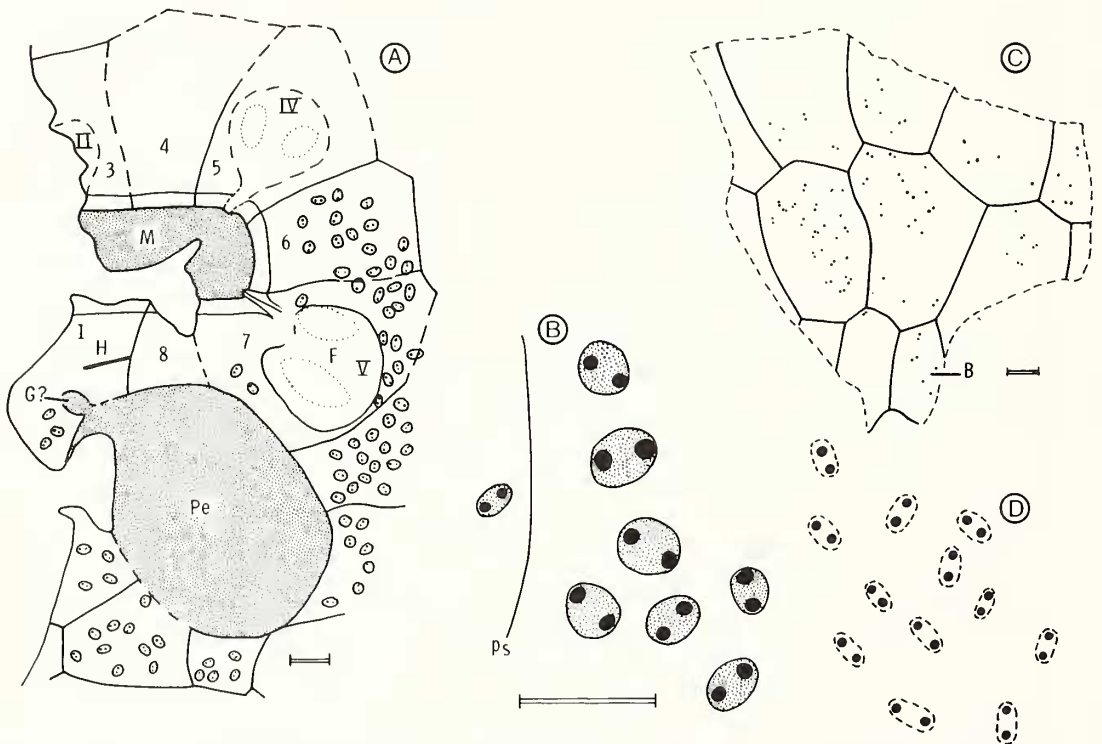
Description. Theca: presumably roughly spherical, about 30–35 mm in diameter, showing the basal portion. Five large lobate basal plates. Base concave, circular, 16 mm in diameter. Theca strongly weathered.

Plates: thick (1.8 mm) with few randomly arranged diplopores.

Diplopores: sparsely developed, small (0.26 × 0.16 mm) possibly with faint rims originally. All other features unknown.

Palaeoecology. The specimen was attached directly in life, probably to a brachiopod. When dead, the cystoid came loose from its attachment, fell over to the side, and was eventually covered by an epifauna of two different types of bryozoa and crinoid roots.

Remarks. This specimen is preserved in a nodular limestone with interbedded shales. The shape of the theca might suggest a sphaeronitid, but the minute and scattered diplopores make it difficult to suggest its affinities. The specimen might be a representative of a new genus, and is at least a new species. Due to lack of information about the oral area, however, I will avoid a new name.



TEXT-FIG. 34. A, B, *Pachycystis norvegica* n. gen., n. sp., PMO 97103, holotype, Kalvsjo Formation, Kalvsjo, Hadeland; A, plates of oro-anal area with peri-orals (1–8), one brachiole facet (F) in each of the four oral corners, a possible gonopore (G?) close to the large periproct (Pe), and a narrow hydropole (H) at the PO1:PO8 suture; B, diplopores. C, D, *Incertae sedis* sp. B., PMO 105.836, Encrinite Limestone, Steinvika, Langesund; C, plates of basal portion, including basals (B); D, diplopores with faintly developed or abraded peripore wall. Scale bar, 1 mm.

Incertae sedis sp. B

Plate 8, fig. 4; text-fig. 34C, D

Material. One specimen, PMO 105.836.

Horizon and locality. Upper Caradoc; within reef complex of Encrinite Limestone, 2 m above base, Steinvika, Langesund.

Description. Theca: only the basal portion showing three plate series is preserved. Maximum height and width both 1.2 mm.

Plates: thick (2.0 mm) with few, randomly arranged diplopores. All plates primary, elongated in ad-aboral direction; most plates hexagonal.

Diplopores: randomly distributed, 0.27 × 0.12 mm, usually strongly abraded; present on all thecal plates, including the basals. All other features unknown.

Palaeoecology. The specimen most probably lived in or very close to the reef environment and was attached directly by its base. Its presence in the crinoid-dominated community suggests that it might have been a low-level suspension feeder, unless it was attached to seaweed. The thick plates rather suggest that the animal was heavy and bottom dwelling.

Remarks. This specimen is preserved in a reef limestone together with crinoids, a few *Heliocrinites* sp., and occasional specimens of *Hemicosmites papaveris*. The weathered state of the specimen and the lack of the oral area makes determination even to family level impossible.

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Geological maps at a scale of 1 : 5000, a list of all fossil localities, drawn sections with occurrences of cystoids and other fossils, and the majority of the described material have been deposited in the Palaeontologisk Museum, Oslo.

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J. FREDRIK BOCKELIE
 Norsk Hydro Research Centre
 Lars Hillesgate
 5000 Bergen, Norway